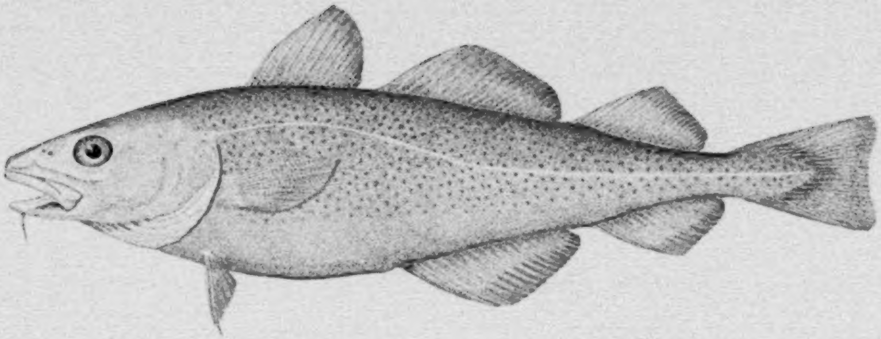
COSEWIC
Assessment and Update Status Report

on the

Atlantic Cod
Gadus morhua

Newfoundland and Labrador population
Laurentian North population
Maritimes population
Arctic population

in Canada



Newfoundland and Labrador population - Endangered
Laurentian North population - Threatened
Maritimes population - Special Concern
Arctic population - Special Concern
2003

COSEWIC
COMMITTEE ON THE STATUS OF
ENDANGERED WILDLIFE
IN CANADA

COSEPAC
COMITÉ SUR LA SITUATION
DES ESPÈCES EN PÉRIL
AU CANADA

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Atlantic Cod — Line drawing of Atlantic cod *Gadus morhua* by H.L. Todd. Image reproduced with permission from the Smithsonian Institution, NMNH, Division of Fishes.

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COSEWIC
Assessment Summary

Assessment summary — May 2003

Common name
Atlantic cod (Newfoundland and Labrador population)

Scientific name
Gadus morhua

Status
Endangered

Reason for designation
Cod in the inshore and offshore waters of Labrador and northeastern Newfoundland, including Grand Bank, having declined 97% since the early 1970s and more than 99% since the early 1960s, are now at historically low levels. There has been virtually no recovery of either the abundance or age structure of cod in offshore waters since the moratoria imposed in 1992 and 1993. Threats to persistence include fishing (now halted), predation by fish and seals, and natural and fishing-induced changes to the ecosystem.

Occurrence
Atlantic Ocean

Status history
The species was considered a single unit and assigned a status of Special Concern in April 1998. When the species was split into separate populations in May 2003, the Newfoundland and Labrador population was designated Endangered. Last assessment based on an update status report.

Assessment summary — May 2003

Common name
Atlantic cod (Laurentian North population)

Scientific name
Gadus morhua

Status
Threatened

Reason for designation
Cod in the Northern Gulf of St. Lawrence and along the south coast of Newfoundland comprise an assemblage of stocks within which there is considerable mixing. They are currently at low levels as a group and overall have declined by about 80% over the past thirty years. However, there is evidence that current levels of abundance are not unprecedented for cod along the south coast of Newfoundland, and the population there has been stable since 1974. Threats to persistence include fishing (now halted in the Northern Gulf), predation by fish and seals, and natural and fishing-induced changes to the ecosystem.

Occurrence
Atlantic Ocean

Status history
The species was considered a single unit and assigned a status of Special Concern in April 1998. When the species was split into separate populations in May 2003, the Laurentian North population was designated Threatened. Last assessment based on an update status report.

Assessment summary — May 2003

Common name
Atlantic cod (Maritimes population)

Scientific name
Gadus morhua

Status
Special Concern

Reason for designation
Cod in the Southern Gulf of St. Lawrence, across the Scotian Shelf and into the Gulf of Maine comprise a heterogeneous assemblage of stocks that are at low levels of abundance as a group. These levels are not unprecedented for the cod in the Southern Gulf, Southwest Scotian Shelf, Bay of Fundy and George's Bank, but those on the Eastern Scotian Shelf are at historic lows and have continued to decline in the absence of directed fishing. Overall, cod in the entire region have declined 14% in the past 30 years, and have demonstrated a sensitivity to human activities. Threats to persistence include directed fishing, bycatch in other fisheries, natural predation, and natural and fishing-induced changes to the ecosystem.

Occurrence
Atlantic Ocean

Status history
The species was considered a single unit and assigned a status of Special Concern in April 1998. When the species was split into separate populations in May 2003, the Maritimes population was designated Special Concern. Last assessment based on an update status report.

Assessment summary — May 2003

Common name
Atlantic cod (Arctic population)

Scientific name
Gadus morhua

Status
Special Concern

Reason for designation
Cod in the Arctic occur mostly in a few coastal salt lakes, and numbers of adults may be no more than a few thousand. Uncertainty with respect to the actual number of locales and populations makes it difficult to assign any higher status, but the known populations are sensitive to human activities. Poorly regulated fishing is a potential threat.

Occurrence
Arctic Ocean

Status history
The species was considered a single unit and assigned a status of Special Concern in April 1998. When the species was split into separate populations in May 2003, the Arctic population was designated Special Concern. Last assessment based on an update status report.

COSEWIC
Executive Summary

Atlantic Cod
Gadus morhua

Species information

Class:	Actinopterygii
Order:	Gadiformes
Family:	Gadidae
Latin binomial:	*Gadus morhua* Linnaeus 1758
Common names:	English — Atlantic cod French — morue franche Inuktitut — ogac (Nunavut); ovak, ogac (Ungava Bay); uugak, ugak (Innu, Labrador) (McAllister et al. 1987)

Distribution

Atlantic cod inhabit all waters overlying the continental shelves of the Northwest and the Northeast Atlantic Ocean. On a global scale, the historical distribution of cod probably differs relatively little from that of its present distribution. In Canada, Atlantic cod are found contiguously along the east coast from Georges Bank and the Bay of Fundy in the south, northward along the Scotian Shelf, throughout the Gulf of St. Lawrence, around the island of Newfoundland, and finally along the eastern shores of Labrador and Baffin Island, Nunavut. There are also several landlocked populations of Atlantic cod on Baffin Island. Outside Canadian waters in the Northwest Atlantic, cod can be found on the northeast and southeast tips of Grand Bank and on Flemish Cap, lying immediately northeast of Grand Bank.

Habitat

During the first few weeks of life, cod exist as eggs, and then as larvae, in the upper 50 metres of the ocean. The primary factors affecting habitat suitability for cod during these early stages of life are probably food availability and temperature. The most critical habitat characteristics for Atlantic cod may be those required during the juvenile stage when cod have settled to the bottom for the first 1 to 4 years of their lives. Evidence suggests that a heterogeneous habitat, notably in the form of vertical structures, such as eelgrass, *Zostera marina*, in near-shore waters, is favoured by juvenile cod because it reduces the risk of predation and may also allow for increased growth. As adults, the habitat requirements of cod become increasingly diverse.

Indeed, it is not clear that older cod have particular depth or bottom-substrate requirements. The primary factors affecting the distribution and habitat of older cod are probably temperature and food supply. From a spawning perspective, it is not known if cod have specific habitat requirements. Cod spawn in waters ranging from tens to hundreds of metres in depth. Perhaps the factor most beneficial to the survival of offspring is the presence of physical oceanographic features that would serve to entrain the buoyant eggs and prevent them from being dispersed to waters poorly suited to larval cod, e.g., waters off the continental shelf. It is highly unlikely that spawning habitat is limiting for Atlantic cod.

Biology

The life history of cod varies a great deal throughout the species' range. In the relatively warm waters at the southern end of its Canadian range (Georges Bank, off the state of Maine) and in the Bay of Fundy, cod commonly attain maturity at 2 to 3 years of age. By contrast, cod inhabiting the Northeast Newfoundland Shelf, eastern Labrador, and the Barents Sea typically mature between 5 and 7 years of age. Size at maturity ranges between 35 and 85 cm in length. The number of eggs produced by a single female in a single breeding season typically ranges from between 300,000 and 500,000 at maturity to several million eggs for females greater than 75 cm in length. Egg diameter, which can show a weak, positive association with body size, ranges between 1.25 and 1.75 mm.

Atlantic cod typically spawn over a period of less than three months in water that may vary in depth from tens to hundreds of metres. Cod are described as batch spawners because of the observation that only 5 to 25% of a female's egg complement is released at any given time (approximately every 2 to 6 days) during a 3- to 6-week spawning period. After hatching, larvae obtain nourishment from a yolk sac until they have reached a length of 1.5 to 2.0 mm. During the larval stage, the young feed on phytoplankton and small zooplankton in the upper 10 to 50 metres of the water column. After the larval stage, the juveniles swim, or 'settle', to the bottom, where they appear to remain for a period of 1 to 4 years. These settlement areas are known to range from very shallow (< 10 m to 30 m) coastal waters to moderately deep (50 to 150 m) waters on offshore banks. After this settlement period, it is believed that the fish begin to undertake the often-seasonal movements (apparently undirected swimming in coastal waters) and migrations (directed movements to and from specific, highly predictable locations) characteristic of adults.

Population sizes and trends

Estimates of the size of the breeding part of the population for Atlantic cod are available from two sources: (1) abundance estimates of the mature part of the population, as derived from a fisheries-dependent model called a Virtual Population Analysis (VPA), and (2) catch rates of fish of reproductive age as determined from fisheries-independent research surveys. The latter estimates tend to be more reliable although the former tend to extend further back in time. The Canadian Department of Fisheries and Oceans (DFO) is the primary source of these abundance data.

Based on COSEWIC's guidelines for assigning status below the species level, and within the empirical and theoretical constructs of Evolutionarily Significant Units (Waples 1991), four populations are identified in the present report and, when data are available, trends in the numbers of breeding individuals are described for each. Each of the populations includes cod found in more than one management unit, as delineated by geographical areas called NAFO (Northwest Atlantic Fishery Organization) divisions. These divisions identify the cod stocks managed by the DFO.

Arctic Population: Cod in this population are those confined to coastal lakes along Frobisher Bay and Cumberland Sound, and those inhabiting the marine environment east and southeast of Baffin Island, Nunavut (NAFO Divisions 0A, 0B). Although little is known about cod inhabiting the marine waters in this area, they may be the ancestral source of the relict landlocked populations (7 are known or suspected) inhabiting lakes that receive intermittent tidal intrusions of salt water. Limited data suggest that the lake populations mature at larger sizes than cod elsewhere in Canadian waters, and that their population sizes are relatively small (numbering hundreds of mature individuals). Although there are no data on temporal trends in abundance, increased angling pressure has been identified as a concern by local inhabitants.

Newfoundland & Labrador Population: Cod in this population inhabit the waters ranging from immediately north of Cape Chidley (northern tip of Labrador) southeast to Grand Bank off eastern Newfoundland. For management purposes, cod in this population are treated as three separate stocks by DFO: (1) Northern Labrador cod (NAFO Divisions 2GH), (2) "Northern" cod, i.e., those found off southeastern Labrador, the Northeast Newfoundland Shelf, and the northern half of Grand Bank (NAFO Divisions 2J3KL), and (3) Southern Grand Bank cod (NAFO Divisions 3NO). Cod in this Population are at historically low levels of abundance. The 3-generation rate of decline experienced by the Newfoundland & Labrador population was 97%.

Laurentian North Population: Cod in this population combine the stocks identified for management purposes by DFO as (1) St. Pierre Bank (NAFO Division 3Ps) and (2) Northern Gulf of St. Lawrence (NAFO Divisions 3Pn4RS). Respectively, these stocks are located north of the Laurentian Channel, along the south coast of Newfoundland and bordering Quebec. Cod in this population are at or near historically low levels of abundance. The 3-generation rate of decline experienced by this population was 81%; most of this decline can be attributed to the Northern Gulf cod stock.

Maritimes Population: Cod in this population combine the stocks identified for management purposes as five separate stocks by DFO: (1) Southern Gulf of St. Lawrence (NAFO Division 4T), (2) Cabot Strait (NAFO Division 4Vn), (3) Eastern Scotian Shelf (NAFO Divisions 4VsW), (4) Bay of Fundy/Western Scotian Shelf (NAFO Division 4X), and (5) cod found on the Canadian portion of Georges Bank (NAFO Division $5Ze_{j,m}$). The 3-generation rate of decline experienced by this population was 14%. There is considerable variation in abundance trends within this population. Southern Gulf cod, which comprise most of the cod in this Population, are at higher levels of abundance than they were 3 generations ago. By contrast, Eastern Scotian

Shelf cod are at historic lows and have continued to decline in the absence of directed fishing over the past decade.

Limiting factors and threats

The primary factor responsible for the decline of Atlantic cod was overfishing. In some areas, reductions in individual growth, attributable to environmental effects or size-selective fishing mortality, may have exacerbated the rate of population decline; in some areas, increases in natural mortality may also have contributed to the decline. It is important to note, however, that there is no evidence to suggest that the rates of growth and natural mortality experienced by cod in the 1980s were unprecedented. Although hypotheses invoking factors other than fishing have been posited, there are inadequate data that would allow for definitive tests of these hypotheses.

The primary biological factors limiting the recovery of Atlantic cod south of Cape Chidley, Labrador, include:

1. Collapsed age structure, loss of spawning components (e.g., the spring-spawning component on the Eastern Scotian Shelf), and/or reduced area occupied by spawners;
2. Below-average recruitment rate in some parts of the range (Southern Grand Bank, St. Pierre Bank, Eastern and Western Scotian Shelf), but not others (NE Newfoundland Shelf, Northern and Southern Gulf of St. Lawrence);
3. Higher-than-expected natural mortality of adults in some parts of the range of each population;
4. Decline in individual growth rate in some areas within each population.

Identifiable threats to the recovery of Atlantic cod include directed fishing (a consequence of the setting of management quotas) and indirected fishing (a consequence of illegal fishing, catch misreporting, discarding, and bycatch from other fisheries). Suspected threats to recovery include altered biological ecosystems, with concomitant changes to the magnitude and type of species interactions, and alterations to bottom habitat. Among these species interactions, seal predation has been implicated as a negative influence on cod recovery in some areas, notably off Newfoundland and Labrador, and in the Northern Gulf of St. Lawrence.

Special significance of the species

Given its historical and contemporary importance to society, few species have been of greater significance in Canada. After the short-lived Viking-based settlements on Newfoundland's Northern Peninsula in the late tenth century, it was cod that brought the first Europeans to Newfoundland waters in the late fifteenth century, an economic venture that spawned one of the first permanent settlements in British North America (1612; Cupids, Newfoundland). Until the early 1990s, Atlantic cod was the economic mainstay for Newfoundland and Labrador, as it was for a large part of the population in the Maritimes and along Quebec's north shore and Gaspé Peninsula. From a biological perspective, the Atlantic cod, which numbered approximately 2.5 billion spawning individuals as recently as the early 1960s, was one of the dominant species of the marine food web in the Northwest Atlantic.

Existing protection or other status designations

In Canada, the Atlantic cod is protected federally by the *Fisheries Act* and by the *Oceans Act*. Several of the cod populations in Canadian waters are managed jointly with other countries. For example, the Georges Bank cod stock (NAFO Division $5e_{j,m}$) is jointly managed by Canada's DFO and the National Marine Fisheries Service in the United States. The cod stocks inhabiting the Newfoundland & Labrador population and the offshore waters of the Arctic population are managed jointly by Canada and international fishing nations, such as Russia, Portugal and Spain, under the auspices of the Northwest Atlantic Fisheries Organization (NAFO).

Other Status Designations for Atlantic Cod: IUCN: Vulnerable
Global Heritage Status Rank: G5

Summary of status report

The report suggests that, for designation purposes, Atlantic cod in Canada be recognized as four Populations, in accordance with known genetic, ecological, and demographic data, and in accordance with the guidelines detailed in Appendix F5 of COSEWIC's Organization and Procedures Manual (Version 16, April 2002).

Regarding the assignment of risk, only the primary cause of the reduction in Atlantic cod (fishing) can be deemed reversible and understood. However, fishing has not ceased in any of the populations (although it is restricted in some parts of some populations, such as the Eastern Scotian Shelf). In the Laurentian North population, excessive fishing mortality has reduced the breeding part of the population, particularly in the Northern Gulf section of this population. For the Newfoundland & Labrador population, it is evident, based on harvest rates estimated by DFO, that fishing is delaying recovery in parts of this population's range.

There are several factors that may influence one's perception of risk and, thus, the assignment of status to Atlantic cod. These include (1) possibility of rescue from neighbouring populations, (2) changes to life history traits, (3) the degree to which census estimates of abundance reflect effective population sizes, and (4) differential responses by stocks to reductions in fishing. These are detailed and discussed in full in the main body of the status report.

The populations, their 3-generation rates of decline, and threats to their recovery are summarized in the table below.

Population	NAFO Management Division(s)	Three-Generation Rate of Decline	Threats
Arctic	0AB	Unknown	Increased angling pressure in some lakes.
Newfoundland and Labrador	2GHJ, 3KLNO	97%	1. Fishing (including legal, illegal, and unreported catches), notably on northern cod. 2. Fishing-induced and natural changes to the ecosystem, resulting in altered levels of inter-specific competition and predation, notably predation by seals and fish on northern cod. 3. Alteration of bottom habitat by fishing gear represents a potential but unevaluated threat.
Laurentian North	3Ps, 3Pn4RS	81%	1. Fishing (including legal, illegal, and unreported catches), representing a greater threat to Northern Gulf cod. 2. Fishing-induced and natural changes to the ecosystem, resulting in altered levels of inter-specific competition and predation, notably predation by seals and fish on Northern Gulf cod. 3. Alteration of bottom habitat by fishing gear represents a potential but unevaluated threat.
Maritimes	4T, 4Vn, 4VsW, 4X, $5e_{j,m}$	14%	1. Fishing (including legal, illegal, and unreported catches), with the exception of Eastern Scotian Shelf cod. 2. Fishing-induced and natural changes to the ecosystem, resulting in altered levels of inter-specific competition and predation, notably on Southern Gulf and Eastern Scotian Shelf cod. 3. Alteration of bottom habitat by fishing gear represents a potential but unevaluated threat.

COSEWIC MANDATE

The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) determines the national status of wild species, subspecies, varieties, and nationally significant populations that are considered to be at risk in Canada. Designations are made on all native species for the following taxonomic groups: mammals, birds, reptiles, amphibians, fish, lepidopterans, molluscs, vascular plants, lichens, and mosses.

COSEWIC MEMBERSHIP

COSEWIC comprises representatives from each provincial and territorial government wildlife agency, four federal agencies (Canadian Wildlife Service, Parks Canada Agency, Department of Fisheries and Oceans, and the Federal Biosystematic Partnership), three nonjurisdictional members and the co-chairs of the species specialist groups. The committee meets to consider status reports on candidate species.

DEFINITIONS

Species	Any indigenous species, subspecies, variety, or geographically defined population of wild fauna and flora.
Extinct (X)	A species that no longer exists.
Extirpated (XT)	A species no longer existing in the wild in Canada, but occurring elsewhere.
Endangered (E)	A species facing imminent extirpation or extinction.
Threatened (T)	A species likely to become endangered if limiting factors are not reversed.
Special Concern (SC)*	A species of special concern because of characteristics that make it particularly sensitive to human activities or natural events.
Not at Risk (NAR)**	A species that has been evaluated and found to be not at risk.
Data Deficient (DD)***	A species for which there is insufficient scientific information to support status designation.

* Formerly described as "Vulnerable" from 1990 to 1999, or "Rare" prior to 1990.
** Formerly described as "Not In Any Category", or "No Designation Required."
*** Formerly described as "Indeterminate" from 1994 to 1999 or "ISIBD" (insufficient scientific information on which to base a designation) prior to 1994.

The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) was created in 1977 as a result of a recommendation at the Federal-Provincial Wildlife Conference held in 1976. It arose from the need for a single, official, scientifically sound, national listing of wildlife species at risk. In 1978, COSEWIC designated its first species and produced its first list of Canadian species at risk. Species designated at meetings of the full committee are added to the list.

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Canada

The Canadian Wildlife Service, Environment Canada, provides full administrative and financial support to the COSEWIC Secretariat.

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Atlantic Cod
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2003

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SPECIES INFORMATION

Name and classification

Class:	Actinopterygii
Order:	Gadiformes
Family:	Gadidae
Latin binomial:	*Gadus morhua* Linnaeus 1758
Common names:	English — Atlantic cod French — morue franche Inuktitut — ogac (Nunavut); ovak, ogac (Ungava Bay); uugak, ugak (Innu, Labrador) (McAllister et al. 1987)

Description

The Atlantic cod is a medium to large marine fish (Figure 1), inhabiting cold (10° to 15° C) and very cold waters (less than 0° to 5° C) in coastal areas and in offshore waters overlying the continental shelf throughout the Northwest and Northeast Atlantic Ocean. Morphologically, the feature that distinguishes cod from most other fishes (a feature shared by other gadids) is the presence of three dorsal fins and two anal fins. Otherwise, cod have the 'classic', streamlined, fusiform shape characteristic of fish that are able to sustain moderate speed over relatively long distances. The colour of cod varies a great deal throughout Canadian waters, having been described by fishers as near-black, brown, and red, depending on the location of capture (Neis et al.1999). The flesh of cod is composed of firm, non-oily, white tissue that deteriorates relatively slowly after death, and is easily preserved by drying, salting, or some combination thereof.

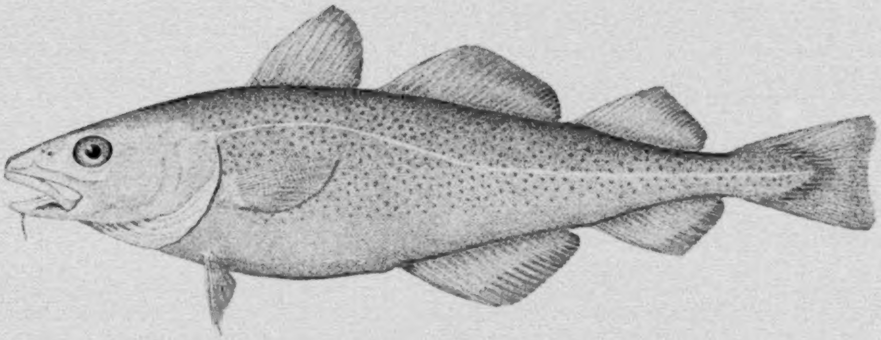


Figure 1. Line drawing of Atlantic cod, or morue franche, *Gadus morhua*, by H.L. Todd. Image reproduced with permission from the Smithsonian Institution, NMNH, Division of Fishes.

Populations

There are two approaches one could adopt in assigning Atlantic cod to an at-risk category. The first, and the one adopted in 1998 when COSEWIC assigned cod to the Special Concern (Vulnerable) category, is to group all cod together and to assign a single designation to cod throughout their entire range in Canadian waters. Such an approach could be defended scientifically if there was no evidence of population differentiation in genetic variation, life history, or ecology throughout the species' range in the Northwest Atlantic. However, available genetic and ecological data are consistent with the hypothesis that Atlantic cod can be distinguished as separate populations, some of which can be combined and potentially recognized as Evolutionarily Significant Units (ESUs).

Heuristically, an ESU is defined by two criteria: 1) it must be substantially reproductively isolated from other conspecific units, and 2) it must represent an important component of the evolutionary legacy of the species (Waples 1991). ESUs are generally more reproductively isolated over a longer period of time than are the populations within them.

Importantly, as Waples (1991) argued, the data required to designate ESUs should include information on genetic, ecological, and life history differences within and among putative ESUs. The reason for this is that one type of information is often insufficient on its own. For example, an absence of selectively-neutral, microsatellite variation between putative populations provides no information on the degree to which populations differ with respect to selectively important genetic variation. And one's interpretation of microsatellite variation must be tempered by potential sampling deficiencies (e.g., lack of information on temporal variability, insufficient sample sizes, use of extraordinarily variable loci). Similarly, geographic differences in life history may simply reflect environmental, rather than genetic, variation.

Combining information from genetic, ecological, and life history research, there is substantial evidence of population differentiation among Atlantic cod in the Northwest Atlantic. However, while differences among cod stocks are sufficiently high to warrant their separate treatment from a management perspective (Smedbol et al. 2002), it is not clear how populations might best be designated as ESUs, given that genetic and life history data are not available for all stocks.

Nonetheless, there is ever-increasing and substantive evidence of adaptive differences among cod at spatial scales considerably smaller than the geographical range of the species in Canada. The limited degree of movement among populations required for adaptive differences to arise is suggested by a series of genetic and mark-recapture studies. From the general perspective, these and other relevant studies include those on:

1. genetic analyses of microsatellite variation (Bentzen et al. 1996; Ruzzante et al. 1996, 1997, 1998, 1999, 2000a,b, 2001; Pogson et al. 2001; Beacham et al. 2002; see Carr et al. [1995] and Carr and Crutcher [1998] for an alternative interpretation, based on mtDNA analyses)

2. mark-recapture data (Templeman 1962; Taggart et al. 1995; Hunt et al. 1999; Brattey et al. 2001a,b)
3. differences in migratory behaviour (Lear 1984; Chouinard et al. 2001; Lilly et al. 2001)
4. spatio-temporal differences in spawning period and location (Myers et al. 1993; Hutchings et al. 1993)
5. differences in otolith trace element composition (Campana et al. 1999)
6. geographic variation in life history (Trippel et al. 1997; McIntyre and Hutchings in press)
7. spatial differences in vertebral number (Templeman 1981), variation demonstrated to have a genetic basis in fishes (e.g., Billerbeck et al. 1997) and to be adaptively significant (e.g., Swain 1992)
8. genetically-based differences in the production of antifreeze proteins (Goddard et al. 1999)
9. genetically based differences in growth rate and food conversion efficiency (Purchase and Brown 2001)
10. genetically based differences in the influence of light intensity on survival and growth rate in early life (Puvanendran and Brown 1998)
11. geographical differences in recruitment, natural mortality and somatic growth (Swain and Castonguay 2000).

The challenge here may not be one of convincing individuals of the utility and scientific justification for identifying ESUs for Atlantic cod; rather, the difficulty will be in finding agreement on the geographical boundaries used to delineate the ESUs that are consistent with the biological data and with COSEWIC's assignment of extinction risk at levels below that of the species. In this context, it is important to acknowledge that an ESU can contain multiple populations, each of which might be connected by some small degree of migration (McElhany et al. 2000).

Based on COSEWIC's guidelines for assigning status below the species level, and within the empirical and theoretical constructs of Evolutionarily Significant Units (Waples 1991), four Populations are identified in the present report and, when data are available, trends in the numbers of breeding individuals are described for each. Each of the Populations includes cod found in more than one management unit, as delineated by NAFO (Northwest Atlantic Fishery Organization) divisions. These divisions also identify the cod stocks managed by the Department of Fisheries and Oceans (DFO).

Arctic population

Cod in this population are those confined to coastal lakes along Frobisher Bay and Cumberland Sound, and those inhabiting the marine environment east and southeast of Baffin Island, Nunavut (NAFO Divisions 0A, 0B). Although little is known about cod inhabiting the marine waters in this area, they may be the ancestral source of relict landlocked populations (at least seven of which are known or suspected) inhabiting lakes that receive intermittent tidal intrusions of salt water.

Newfoundland and Labrador population

Cod in this population inhabit the waters ranging from immediately north of Cape Chidley (the northern tip of Labrador) southeast to Grand Bank off eastern Newfoundland. For management purposes, cod in this population are treated as three separate stocks by DFO: (1) Northern Labrador cod (NAFO Divisions 2GH), (2) "Northern" cod, i.e., those found off southeastern Labrador, the Northeast Newfoundland Shelf, and the northern half of Grand Bank (NAFO Divisions 2J3KL), and (3) Southern Grand Bank cod (NAFO Divisions 3NO). Approximately 75% to 80% of the Atlantic cod in Canadian waters were located within this Population in the early 1960s.

Laurentian North population: Cod in this population combine the stocks identified for management purposes by DFO as (1) St. Pierre Bank (NAFO Division 3Ps) and (2) Northern Gulf of St. Lawrence (NAFO Divisions 3Pn4RS). These stocks are located north of the Laurentian Channel, bordering the south coast of Newfoundland and Quebec, respectively.

Maritimes population

Cod in this population combine the stocks identified for management purposes as five separate stocks by DFO: (1) Southern Gulf of St. Lawrence (NAFO Division 4T), (2) Cabot Strait (NAFO Division 4Vn), (3) Eastern Scotian Shelf (NAFO Divisions 4VsW, (4) Bay of Fundy/Western Scotian Shelf (NAFO Division 4X), and (5) cod found on the Canadian portion of Georges Bank (NAFO Division $5Ze_{j,m}$). Geographically, these stocks are located in the waters adjacent to the three Maritime provinces, extending from the southern Gulf of St. Lawrence south to the Canadian portion of Georges Bank.

Scientific basis for distinguishing the Newfoundland & Labrador, Laurentian North, and Maritimes populations

These populations can be distinguished from one another by a combination of different types of data. These include age at maturity, maximum population growth rate (r_{max}), temporal trends in abundance, genetic variability at selectively neutral loci, and genetic differences among selectively important traits.

1. Age at maturity

Age at maturity (represented as the age at which 50% of females are reproductive) differs among the populations, particularly between the Newfoundland & Labrador population and the other two populations. To compare ages at maturity, I calculated the average age across all stocks within each population, weighting the average age for each stock by the highest estimated abundance of mature individuals in that stock (as determined by VPA abundance data; see POPULATION SIZES AND TRENDS below). Cod are oldest at maturity in the Newfoundland & Labrador population in which both stocks mature at 6 years, and youngest in the Maritimes population in which 2 of the 5 stocks mature at 2.5 years.

Population	Number of stocks	Age at maturity (range among stocks)	Reference(s)
Newfoundland & Labrador	2	6.0 (6-6 yr)	Lilly et al. (1991); Trippel et al. (1997); Stansbury et al. (2001)
Laurentian North	2	4.5 (4-6 yr)	Brattey et al. (2001a); Yvon Lambert, personal communication
Maritimes	5	4.3 (2.5-4.5 yr)	Trippel et al. (1997); Doug Swain, personal communication; Hunt and Hatt (2002)

2. Maximum population growth rate (r_{max})

Based on data available in the mid-1990s, one can compare estimates of maximum population growth for the populations identified here. The estimate for northern cod is available from Hutchings (1999); the remaining estimates are reported by Myers et al. (1997a; revised Table 1 [from which the present estimates of *r* were obtained] can be obtained from Ransom Myers, Department of Biology, Dalhousie University, Halifax, NS B3H 4J1). These estimates are subject to the caveat that r_{max} may have changed since the mid-1990s. However, what is important here is the question of whether r_{max} is likely to differ among the populations, even for data restricted to the pre-collapse and immediate post-collapse periods for each stock.

To compare r_{max} among populations, I calculated the average r_{max} across all stocks within each population, weighting the r_{max} estimate for each stock by the highest known abundance of mature individuals in that stock (as determined by VPA abundance data; see POPULATION SIZES AND TRENDS below). As one would predict, based on their differences in age at maturity, the Newfoundland & Labrador population has a lower maximum population growth rate than its two more southerly counterparts.

Population	Number of stocks	Maximum population growth rate, r_{max} (range among stocks)	Reference(s)
Newfoundland & Labrador	2	0.15 (0.13-0.35)	Myers et al. (1997, revised Table 1); Hutchings (1999)
Laurentian North	2	0.32 (0.29-0.39)	Myers et al. (1997, revised Table 1)
Maritimes	5	0.31 (0.24-0.67)	Myers et al. (1997, revised Table 1)

3. Temporal abundance trends

There is a concordance in the temporal abundance trends of the cod stocks that comprise the Newfoundland & Labrador population that is not evident throughout all parts of the ranges of the other populations. All cod in the Newfoundland & Labrador Population have experienced steady declines across the entire time period of available data and are currently at historic low levels of abundance (see POPULATION SIZES AND TRENDS below). In contrast, the current low levels of cod in parts of the other two populations have been experienced previously and are not, thus, unprecedented.

4. Genetic differentiation at selectively neutral loci

There is strong evidence of genetic differentiation at selectively neutral loci among the populations. Based on an analysis of 1,300 cod at 5 microsatellite loci, Ruzzante et al.'s (1998) estimates of genetic differentiation were either highest (R_{st}), or among the highest (F_{st}), when comparing cod sampled north and south of the Laurentian Channel, which separates the Newfoundland & Labrador and Laurentian North populations from the Maritimes population. Pogson et al.'s (2001) analysis of 10 nuclear restriction-fragment-length-polymorphism (RFLP) loci also revealed significant genetic differences among cod sampled from the populations. In addition, Pogson et al. (2001) reported a highly significant negative association between gene flow and geographic distance among cod sampled in the Canadian waters from the Newfoundland & Labrador and Maritimes populations, an association also reported by Beacham et al. (2002) from their analysis of 7 microsatellite loci and a pantophysin locus. These negative associations imply that the greater the geographical separation of cod, the lower their genetic affinity. Additional evidence for genetic differentiation among the populations at selectively neutral loci is summarized in the table below.

For the most part, the reduced gene flow that one can infer from these genetic studies are supported by tagging studies that have been conducted since the 1950s (Taggart et al. 1995). Templeman (1962), for example, reported that "there do not appear to be any migration tracks or any considerable intermingling across [the Laurentian] Channel and stocks on each side of the Channel are thus separate." Although recent tagging studies (Brattey et al. 2001a,b) have suggested that cod from the St. Pierre Bank stock of the Laurentian North population intermingle with those in the southern portion of the Newfoundland & Labrador population, the genetic research cited above and in the summary table below suggests that migrants are not particularly successful reproductively.

Summary of the evidence for genetic differentiation among the Newfoundland & Labrador, Laurentian North, and Maritimes populations, based on studies of selectively neutral loci and selectively important traits.

Population	Laurentian North	Maritimes
Newfoundland & Labrador	1. Seven microsatellite loci and one pantophysin locus (Beacham et al. 2002) 2. Five microsatellite loci (Ruzzante et al. 1998)	1. Six microsatellite loci (Bentzen et al. 1996) 2. Five microsatellite loci (Ruzzante et al. 1998) 3. Ten nuclear restriction-fragment-length-polymorphism (RFLP) loci (Pogson et al. 2001) 4. Influence of light on survival and growth (Puvanendran and Brown 1998). 5. Growth rate and food conversion efficiency (Purchase and Brown 2001)
Laurentian North	NA	1. Six microsatellite loci (Ruzzante et al. 2000) 2. Five microsatellite loci (Ruzzante et al. 1998) 3. Larval growth and survival (Hutchings et al. MS2002)

5. Genetic differentiation among selectively important traits

In addition to differences at selectively neutral loci, there is increasing evidence that cod in the Northwest Atlantic differ from one another at loci that are under selection. This inference is drawn from experiments in which differences among cod populations have been documented after the effects of the environment have been removed from the analysis.

Among reports in the published literature, Goddard et al. (1999) found that cod in the northern part of the Newfoundland & Labrador population produced higher levels of anti-freeze protein (which prevents ice crystals from forming in the blood at sub-zero degree temperatures) than cod further south in the same population, a difference that almost certainly would be magnified if one were to compare anti-freeze protein production in cod that never experience sub-zero degree water temperatures, e.g., those throughout most of the Laurentian North and Maritimes populations. Comparing cod from the southern portion of the Maritimes population with those from the Newfoundland & Labrador population, genetic differences have also been documented in growth rate and food conversion efficiency (Purchase and Brown 2001), and in the influence of light intensity on survival and growth in early life (Puvanendran and Brown 1998).

There is additional evidence for genetic differences among traits of importance to fitness between cod from the Laurentian North and Maritimes populations (Hutchings et al. MS2002, unpublished data). To assess the genetic basis of phenotypic variation in Atlantic cod, colleagues at the Department of Fisheries and Oceans (Moncton) and at Memorial University of Newfoundland and I are conducting "common-garden" experiments in which cod from putatively different populations are reared under the same environmental conditions in the laboratory. Statistically significant group-level differences in the average expression of a trait, or its interaction with an environmental variable, would suggest that population differences have a genetic and, for fitness-related traits, adaptive basis.

To date, we have undertaken experiments on cod sampled from the Laurentian North (St. Pierre Bank) and Maritimes populations (Southern Gulf of St. Lawrence, Western Scotian Shelf/Bay of Fundy). Population differences in fitness-related traits for cod larvae and juveniles were quantified at two levels of food (1,000 and 4,500 prey/L) and temperature (7° and 11° C), four replicates per treatment.

Preliminary analyses reveal significant main and interaction effects of temperature, food, and population on larval growth and survival. Average growth rate differed significantly among populations ($F=68.03$, $p<0.0001$); larvae from the southernmost population were smallest at 43 days post-hatch whereas larvae from the northernmost population were largest, a pattern consistent with the hypothesis of adaptive variation in growth rate (see Purchase and Brown 2001). A significant temperature×population interaction ($p=0.0003$) on growth suggests a genetic difference in plasticity among populations. Significant population× food ($p=0.008$) and population×temperature interactions ($p=0.025$) also suggest that the effects of food and temperature on larval survival differ genetically among populations.

Given this evidence of genetically based differences in selectively important traits for cod sampled from the Laurentian North and Maritimes populations, it is reasonable to conclude that these differences will be maintained, if not increased, when cod from the Newfoundland and Labrador population are similarly analysed (these experiments will begin in May 2003).

DISTRIBUTION

Global range

Atlantic cod inhabit all waters overlying the continental shelves of the Northwest and the Northeast Atlantic Ocean. In the west, cod extend from waters just south of Georges Bank northward to Baffin Island, Nunavut, Canada (Figure 2). In the Northeast Atlantic, cod range from the North Sea northward through the Norwegian Sea to the Barents Sea off Norway and northern Russia. Cod are also found in abundance in the Skaggerak and Kattegak, the strait separating Scandinavia from Denmark, and in the southern parts of the Baltic Sea. On a global scale, the historical distribution of cod probably differs relatively little from that of its present distribution.

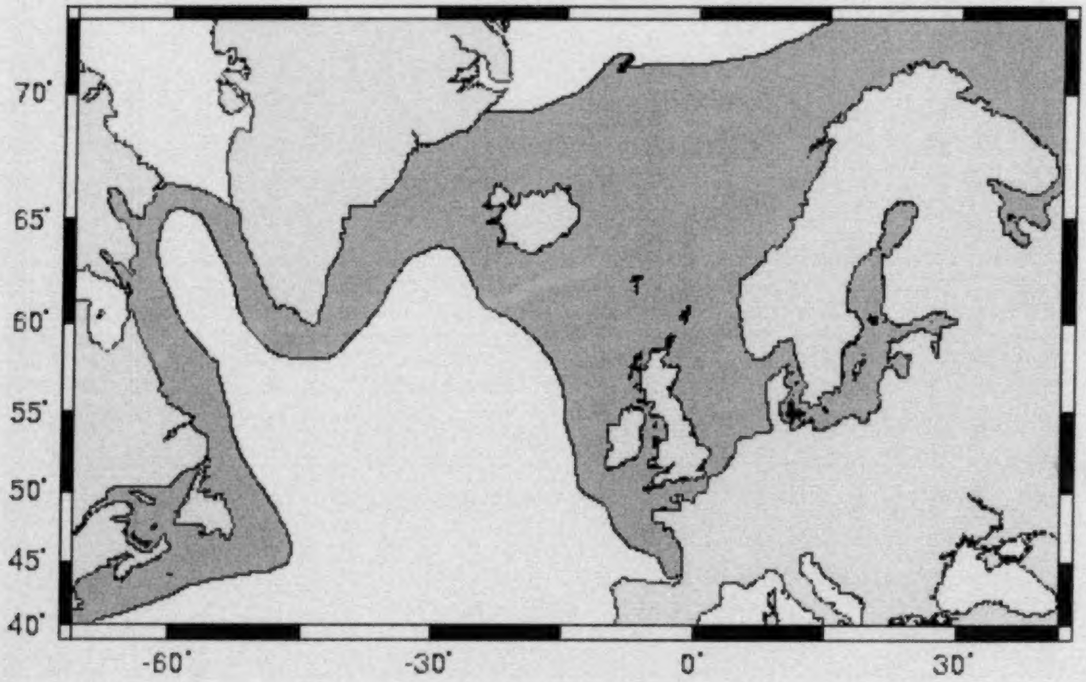
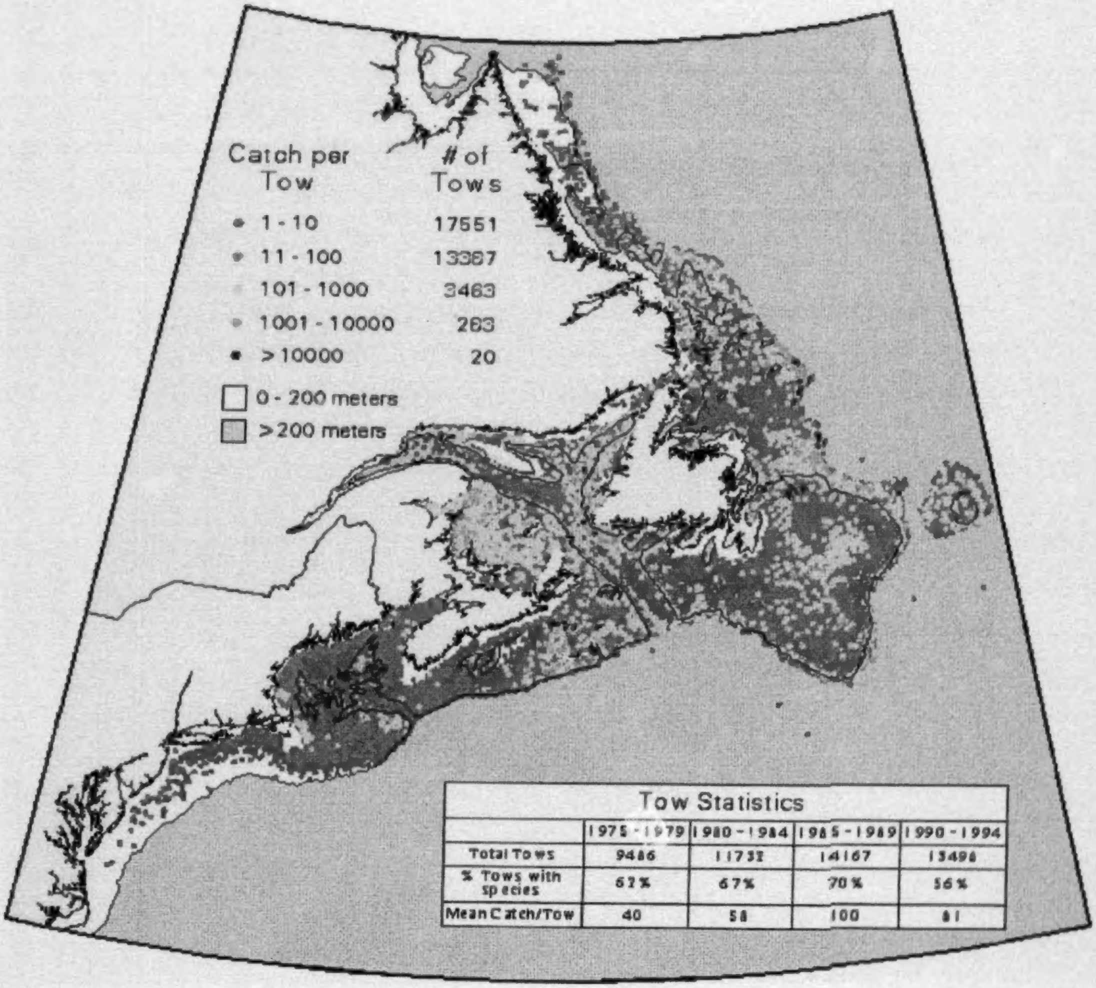


Figure 2. Global distribution of Atlantic cod.

Canadian range

In Canada, Atlantic cod are found contiguously along the east coast from Georges Bank and the Bay of Fundy in the south, northward along the Scotian Shelf, throughout the Gulf of St. Lawrence, around the island of Newfoundland, and finally along the east coasts of Labrador and Baffin Island, Nunavut (Figures 2 and 3). There are also several landlocked populations of Atlantic cod on Baffin Island (McLaren 1967; Patriquin 1967; Table 1). Outside Canadian waters, cod can be found on the northeast and southeast tips of Grand Bank and on Flemish Cap, lying immediately northeast of Grand Bank.

In addition to these offshore waters (typically at depths less than 500 metres), cod can also be found throughout the coastal, inshore waters of Atlantic Canada. The best-studied of these is probably the small, resident Gilbert Bay population in southern Labrador (Green and Wroblewski 2000; Morris and Green 2002), a population that is geographically and genetically distinct from cod inhabiting the offshore waters in this area (Ruzzante et al. 2000; Beacham et al. 2002). Local ecological knowledge, based on interviews with fishers conducted by the Department of Fisheries and Oceans in concert with the Fishermen and Scientists Research Society in the Maritimes, suggests that local, inshore spawning aggregations of cod along coastal Nova Scotia were fewer in number in the late 1990s compared with earlier years.



Catch per Tow	# of Tows
● 1 - 10	17551
● 11 - 100	13387
● 101 - 1000	3463
● 1001 - 10000	283
● >10000	20

☐ 0 - 200 meters
▨ >200 meters

Tow Statistics				
	1975 - 1979	1980 - 1984	1985 - 1989	1990 - 1994
Total Tows	9486	11732	14167	13498
% Tows with species	62%	67%	70%	56%
Mean Catch/Tow	40	58	100	81

Figure 3. Distribution of Atlantic cod in North America from the southern extreme of the species' range to northern Labrador, as determined from fisheries independent surveys conducted by the Canadian Department of Fisheries and Oceans and the National Marine Fisheries Service in the United States. Dots represent survey catch rate data from 1975 to 1994.

The extent of occurrence of Atlantic cod in Canadian waters is probably on the order of 1.1 million square kilometers, an area larger than Ontario, and an area slightly smaller than Quebec. The extent of occurrence has either remained stable over the past four decades (and earlier) or it has declined. Area of occupancy appears to have declined in the areas where such measurements are possible (see POPULATION SIZES AND TRENDS below).

HABITAT

Habitat requirements

Knowledge of the habitat requirements of Atlantic cod is rather poor. Despite the paucity of data, it is reasonable to predict that habitat requirements change significantly with age in this species. With the exception of the few cod that have been observed *in situ*, the following information is based on the sampling of cod at various life stages from different depths and different areas of the ocean.

During the first few weeks of life, cod exist as eggs, and then as larvae, in the upper 10 to 50 metres of the ocean. The primary factors affecting habitat suitability for cod during these early stages of life are probably food availability and temperature (the lower the temperature, the longer the development time, and the longer the period of time during which cod are at sizes that make them highly vulnerable to predation).

The most critical habitat characteristics for Atlantic cod may be those required during the juvenile stage when cod have settled to the bottom for the first 1 to 4 years of their lives. Several studies suggest that a heterogeneous habitat, notably in the form of vertical structures, such as eelgrass, *Zostera marina*, in nearshore waters, is favoured by juvenile cod (e.g., Gotceitas et al. 1995, 1997; Tupper and Boutilier 1995; Gregory and Anderson 1997). Based on observational studies (Tupper and Boutilier 1995) and on experimental manipulations (Gotceitas et al. 1995; Linehan et al. 2001), physically heterogeneous habitat appears advantageous to juvenile cod because it reduces the risk of predation and may also allow for increased growth.

Offshore, it is logical to assume that physical structure would also reduce predator-induced mortality of juvenile cod. For example, video recorded on a submersible during an August 2001 survey of deep, continental-slope waters off southwestern Nova Scotia revealed juvenile cod amongst the extensive growths of deep-sea corals (personal communication, Anna Metaxas, Department of Oceanography, Dalhousie University, Halifax, Nova Scotia).

As cod grow older, it appears as though their habitat requirements become increasingly diverse. Indeed, it is not clear that older cod have particular depth or bottom-substrate requirements. The primary factors affecting the distribution and habitat of older cod are probably temperature and food supply. In a general sense, it appears that cod tend to avoid cold temperatures.

But what is cold for cod in one area is evidently not cold for cod in other areas. For example, it is widely believed that cod migrate out of the southern Gulf of St. Lawrence in autumn to avoid the cold water temperatures in the Gulf during winter (Campana et al. 1999). However, cod off eastern Newfoundland, notably those that overwinter in inshore waters, exist at temperatures below 0°C (Goddard et al. 1999). Perhaps the most reasonable explanation for these apparent differences in water temperature tolerance is that cod in different areas are adapted to their local environments. This conclusion is supported by the finding that cod in different areas of coastal Newfoundland possess different levels of antifreeze protein (see Physiology section below), a physiological adaptation that would influence the tolerance of cod to low water temperatures.

From a spawning perspective, it is not known if cod have specific habitat requirements. Cod spawn in waters ranging from tens (Smedbol and Wroblewski 1997) to hundreds of metres in depth (Hutchings et al. 1993). Atlantic cod in Canadian waters are known to spawn extensively throughout the inshore, nearshore, and offshore waters (McKenzie 1940; Scott and Scott 1988; Hutchings et al. 1993; Morgan and Trippel 1996), a conclusion also supported by fishers (Neis et al. 1999). Although cod spawning appears to be associated with the bottom (Morgan and Trippel 1996; Hutchings et al. 1999), this may have more to do with the cod mating system (a lek mating system has been hypothesized; Hutchings et al. 1999; Nordeide and Folstad 2000) rather than any physical requirements for the offspring, given that cod neither build egg nests nor provide parental care. Perhaps the factor most beneficial to the survival of their offspring is the presence of physical oceanographic features (e.g., water currents) that would serve to entrain the buoyant eggs and prevent them from being dispersed to waters poorly suited to larval cod, e.g., waters off the continental shelf. It is highly unlikely that spawning habitat is limiting for Atlantic cod.

Thus, the habitat most likely to be critical and potentially limiting for Atlantic cod may well be the vertical, 'three-dimensional' structures provided by plants, rocks, physical relief, and corals. In addition to providing protection from predators, such physical heterogeneity would almost certainly provide habitat for small fish and invertebrates, organisms upon which juvenile cod could feed.

Trends

If physical structure is critically important to the survival of juvenile cod, notably in the form of plants, bottom physical relief, and corals, there may be less habitat available today than decades ago in some parts of the range of this species. Any reduction in physical heterogeneity on the bottom since the 1960s can be attributed to the increased use of bottom-trawling gear to catch groundfish such as cod, haddock, pollock, and several species of flatfish. Repeated trawling in a given area tends to 'smooth' and flatten the bottom, reducing vertical and physical heterogeneity (Collie et al. 1997, 2000; Kaiser and de Groot 2000). The destruction of deep-dwelling corals off Nova Scotia—first reported and well-documented by fishermen—is another product of bottom-trawling and, to a considerably lesser degree, long-lining (Mortensen et al. submitted). Although physically heterogeneous areas frequented by juvenile cod may not have been heavily trawled where gear damage or loss was likely, no studies have been undertaken to evaluate the effects of trawling on the quantity and quality of juvenile cod habitat.

BIOLOGY

General

Despite having been fished for more than 500 years in Canadian waters, there remain large gaps in our knowledge of many of the most basic elements of the biology and ecology of this species. Nonetheless, it is known that after hatching, a period of time that takes approximately 60 degree-days, the larvae obtain nourishment from a yolk sac until they have reached a length of 1.5 to 2.0 mm. During the larval stage, the young feed on phytoplankton and small zooplankton in the upper 10 to 50 metres of the water column. After a few weeks, the larvae swim, or 'settle', to the bottom, where they appear to remain for a period of 1 to 4 years throughout most of the species' Canadian range. These settlement areas are known to range from very shallow (< 10 m to 30 m) coastal waters to moderately deep (50 to 150 m) waters on offshore banks. In addition to providing food, these settlement areas almost certainly provide habitat that provides the larval and juvenile cod protection from predators. After this settlement period, it is believed that the fish begin to undertake the often-seasonal movements (apparently undirected swimming in coastal waters) and migrations (directed movements to and from specific, highly predictable locations) characteristic of adults. Anecdotal reports suggest that very large adults (> 100 cm) may not migrate as extensively as smaller adults.

Reproduction: Life history variation

The life history of cod varies a great deal (Myers et al. 1996; McIntyre and Hutchings in press). Most life history traits, such as age and size at maturity, longevity, and size-specific fecundity differ greatly among populations, while some, such as egg size, appear to be similar throughout the species' range. As with most indeterminately growing organisms (those that continue to increase in size after maturity), fecundity (the number of eggs per female per breeding season) increases with body size. In cod, as with most fish, the number of eggs per female generally increases with body mass as a power function. Body size at a given age is a function of growth rate, a parameter that varies greatly among cod populations, being relatively slow in the north and fast in the south. In turn, growth rate of cod is a function of temperature, food supply, density, and the proportional allocation of energy to reproduction.

In the relatively warm waters at the southern end of its Canadian range (Georges Bank, off the state of Maine) and in the Bay of Fundy, cod commonly attain maturity at 2 to 3 years of age (Trippel et al. 1997; McIntyre and Hutchings in press). By contrast, cod inhabiting the Northeast Newfoundland Shelf, eastern Labrador, and the Barents Sea reproduce for the first time between 5 and 7 years of age (Myers et al. 1997b; Smedbol et al. 2002). One consequence of these population differences in age at maturity is population variation in generation time. However, when providing an estimate of generation time, one needs to be cognizant of the fact that generation time has almost certainly changed over time for Atlantic cod. This can be attributed to apparent reductions in age at maturity in some populations (Trippel et al. 1997) and to reductions in longevity. For example, in the early 1960s, it is estimated that more than 50% of the eggs produced by Newfoundland's northern cod stock were produced by females 10 years of age and older (Hutchings and Myers 1994). By the late 1980s, this age class is estimated to have contributed less than 10% of the eggs. In the late 1990s and as recently as autumn 2000, females older than age 10 were not sampled by DFO surveys of the northern cod stock (Lilly et al. 2001).

Size at maturity can also differ significantly among cod populations. On average, length at maturity typically ranges between 45 and 55 cm. Smaller sizes at maturity have been reported in recent years for Eastern Scotian Shelf cod (33-37 cm; Paul Fanning, DFO, Bedford, NS, personal communication) and for cod in the genetically isolated population inhabiting Gilbert Bay, Labrador (31-42 cm; Morris and Green 2002). At the other extreme, length at maturity has been reported to be as large as 65 cm for males and 85 cm for females in Ogac Lake, Baffin Island (Patriquin 1967). The number of eggs produced by a single female in a single breeding season typically ranges from between 300,000 and 500,000 at maturity to several million for females greater than 75 cm in length. There is recent evidence that size-specific fecundity, that is, the number of eggs produced per unit of body mass, differs significantly among cod populations in the Northwest Atlantic and within populations over time (McIntyre and Hutchings in press). Egg diameter, which shows a weak, positive association with body size, ranges between 1.25 and 1.75 mm (Chambers and Waiwood 1996).

Reproduction: Spawning behaviour

Atlantic cod typically spawn over a period of less than three months (Brander 1994; Chambers and Waiwood 1996; Kjesbu et al. 1996) in water that may vary in depth from tens (Smedbol and Wroblewski 1997) to hundreds of metres (Brander 1994; Morgan et al. 1997). Although individuals are assumed to breed annually, Atlantic cod are described as batch spawners because of the observation that only 5 to 25% of a female's egg complement is released at any given time during her 3- to 6-week spawning period (Chambers and Waiwood 1996; Kjesbu et al. 1996). Spawning intervals of 2 to 6 days appear typical of individual females held in captivity (Kjesbu 1989; Chambers and Waiwood 1996; Kjesbu et al. 1996).

The behaviour that immediately precedes the release of sperm and eggs was initially documented at nineteenth century Atlantic cod hatcheries in Newfoundland (Templeman 1958) and Norway (Dannevig 1930). These observations, and those of Brawn (1961), describe a "ventral mount" in which the male, while grasping the female with his pelvic fins and matching her swimming speed, positions himself beneath the female with the urogenital openings of both fish opposite one another.

Based on the only two papers in the primary scientific literature that have reported cod behaviour during spawning (Brawn 1961; Hutchings et al. 1999), successful reproduction in Atlantic cod involves a complex repertoire of behaviours within and between sexes. Spawning male cod appear to establish a dominance hierarchy, with rank determined by aggressive interactions, particularly chases of one male by another, and possibly by body size, larger individuals often being dominant over smaller individuals. Agonistic interactions, continuing through the spawning season, may allow high-ranking males to defend territories. Limited genetic data suggest that male fertilization success increases with male body size and/or behavioural dominance (Hutchings et al. 1999) and that eggs from a single reproductive bout can be fertilized by more than one male (Hutchings et al. 1999; Rakitin et al. 2001). Based on these genetic data, and on the direct observation of spawning behaviour by cod from southern Nova Scotia and the Southern Gulf of St. Lawrence (S. Rowe and J.A. Hutchings, unpublished data), it is reasonable to assume that satellite males, adopting a 'sneak' form of mating, are a regular feature of cod reproduction and that satellite males are able to fertilize some of the eggs released by a female during a spawning. The phenotypic and behavioural correlates of reproductive success in Atlantic cod are currently being examined in a series of spawning experiments being conducted at Dalhousie University by the author.

Hutchings et al. (1999) hypothesized that interactions between sexes are consistent with the hypothesis that females, and possibly males, exercise mate choice. One prominent behaviour observed in large experimental tanks is the circling of individual females by individual males on or near the bottom (Hutchings et al. 1999; Skjæraasen et al. submitted). Several factors associated with this circling behaviour are suggestive of female mate choice. Firstly, these circling bouts are initiated and terminated by females. Secondly, by restricting circling to occasions when they are positioned directly on the bottom, females can effectively prevent ventral mounts by circling and non-circling males. Thirdly, circling provides females the opportunity to be in close physical contact with, and assess the quality of, several males prior to spawning. Hutchings et al. (1999) have also hypothesized that females may be choosing males on the basis of the sounds produced by male gadids during spawning (Brawn 1961; Hawkins and Amorim 2000; Nordeide and Folstad 2000). Acoustic communication in cod is facilitated by drumming muscles whose rapid vibrations against the air bladder are capable of producing low-frequency sounds audible to other cod. Preliminary analyses suggest that the size of a male's drumming muscle, relative to that male's body size, may be positively associated with mating success and may differ among populations (S. Rowe and J.A. Hutchings unpublished data).

Survival

The high fecundity of Atlantic cod (ranging from several hundred thousand to several million eggs per female per breeding season) represents a life history adaptation by cod that allows them to adopt the reproductive strategy of releasing eggs directly into the water column and of providing these eggs with no protection, either through the construction of egg nests or through the provision of parental care. This strategy of maximizing the production of eggs the sizes of which approach, or attain, the physiological minimum for survival has been interpreted as an adaptive response to environments in which egg size confers no consistent, inter-generational advantage to survival in early life (Hutchings 1997).

The high-fecundity strategy adopted by Atlantic cod is an evolutionary response to the exceedingly high mortality associated with such a reproductive strategy. Based on estimates of fecundity, weight-at-age, and age-specific abundance of northern cod, Hutchings (1999) estimated that survival from birth until the age of 3 years averaged 1.13×10^{-6}, or approximately one in one million, for the cohorts of cod born from 1962 to 1988. Between the ages at which cod first become vulnerable, or are recruited, to the commercial fishery (varying between 1 and 3 years for Canadian stocks of cod, being younger in the south) and the age at death, the annual mortality probability of cod, independent of age and size, has been estimated to be 18% (Pinhorn 1975).

Prior to the closure of most fisheries to targeted or directed fishing in the early 1990s (July 1992, for northern cod; January 1994, for northern Gulf cod; September 1993, for all other stocks except Western Scotian Shelf/Bay of Fundy cod and Georges Bank cod, neither of which ever closed), fishing was the dominant source of mortality for Atlantic cod. At one extreme, it is estimated that fishing removed annually more than 70% of Newfoundland's northern cod available to be caught in the late 1980s and early 1990s (Baird et al. 1992; Hutchings and Myers 1994). Fishing remains a primary source of mortality for parts of the Newfoundland & Labrador, Laurentian North, and Maritimes Populations (Smedbol et al. 2002). In some areas, most of the mortality experienced by Atlantic cod, at all life stages, can probably be attributed primarily to predation by fish and marine mammals, and secondarily to predation by invertebrates and birds (Bundy et al. 2000; McLaren et al. 2001). Nonetheless, fishing still remains a sizeable source of mortality in many areas, a result of directed fishing quotas and bycatches.

With the exception of cod along one section of the south coast of Newfoundland (NAFO Division 3Ps), cod populations have grown little since the initial closure of the targeted fishing activities almost a decade ago. Although contrary to predictions of rapid recovery made in the early 1990s (detailed by Hutchings et al. 1997), slow rates of population growth following collapses in population size are not atypical when one compares recovery rates for collapsed marine fish stocks worldwide (Hutchings 2000), even when one accounts for reductions in fishing mortality (Hutchings et al. 2001a; Denney et al. submitted). The reasons for slower-than-expected rates of population growth are not known with certainty, although they may include one or more of the following: management failure to reduce to fishing mortality to nil; changes to species community composition with concomitant changes to competitive interactions and predator-prey relationships; reduction in critical habitat; reductions in fertilization rates and/or social interactions necessary for successful reproduction with reductions in fish density.

The relatively slow rates of population growth may be a product of what is known in the fisheries literature as 'depensation' (Myers et al. 1995), and what is known throughout the ecological literature as 'The Allee Effect'. Both refer to situations in which per-capita rates of population growth decline, rather than continually increase, when population sizes fall below some 'threshold' level of abundance. The existence of an Allee Effect has been suggested as one explanation for the relatively slow recovery of Atlantic cod and other marine fishes (Shelton and Healey 1999; Frank and Brickman

2000; Hutchings 2000, 2001a,b; De Roos and Persson 2002). It is worth noting, however, that the observed population growth rates of cod may not be unduly slow, if one incorporates stochastic, or unpredictable, variation in the parameters used to model population growth for Atlantic cod, rather than basing one's predictions on deterministic models (in which all model parameters are fixed). Hutchings (1999) undertook such a modelling exercise for northern cod. Based on his findings, and given the relatively slow rates of individual growth (weight-at-age) and comparatively old age at maturity experienced by northern cod, the observed rate of recovery of northern cod (indeed lack thereof) may not be unexpected.

If resource managers had been consistent in their setting of quotas for the collapsed cod fisheries, and had permitted no targeted or incidental fishing of cod in the past 10 years, the recovery rates for some cod stocks would almost certainly have been greater than what has been observed. One example will serve to illustrate this point. Between 1981 and 1989, the annual quota for northern cod never fell below 200,000 tonnes (1 metric tonne is equal to 1,000 kilograms) (Lilly et al. 2001). A number of fishing industry observers and government resource managers have assumed that considerably smaller quotas would not harm the recovery of this stock. In 1999 and 2000, the quotas for northern cod were 9,000 and 7,000 tonnes, respectively (Lilly et al. 2001), approximately 97% less than the quotas of the mid-1980s. Despite their low levels, these quotas have resulted in rates of fishing mortality sufficiently high to negatively affect stock recovery (these are presented below; see LIMITING FACTORS AND THREATS), providing clear evidence that small quotas can negatively affect the recovery of fish stocks when the stocks themselves are at historically small sizes.

Physiology

From a physiological perspective, the environmental variable of greatest import to Atlantic cod is probably water temperature. It has been suggested that cod will actively avoid waters deemed to be low in temperature. For example, avoidance of cold water is the primary reason given for the autumnal migration of cod out of the Southern Gulf of St. Lawrence to the northeast waters off Cape Breton (Campana et al. 1999). And there is a sound empirical basis for believing that temperature selection by cod should be density-dependent, with the optimal temperature for growth declining as food ration declines (Swain and Kramer 1995).

Although cod are generally found in waters ranging in average annual temperature from 2 to 11° C (Brander 1994), it is clear that cod in some areas off Newfoundland are able to withstand temperatures as low as -1.5° C (Goddard et al. 1999). This temperature is below that (-0.5 to - 0.8° C) at which ice crystals form in the blood. Cod are able to withstand such cold waters, and to prevent the formation of ice crystals in the blood, by producing plasma antifreeze proteins or glycoproteins (AFGPs) that improve freeze resistance. Interestingly, there appears to be an effect of size and/or age on the ability of cod to withstand sub-zero-degree waters. For example, Goddard and Fletcher (1994) reported that juvenile cod (10-40 cm) produce approximately twice as much AFGP as adult cod.

Some of the best evidence that Atlantic cod are adapted to local environments at scales considerably smaller than those corresponding to the NAFO divisions is physiological in nature. In a common-garden experiment in which all individuals were reared under the same environmental conditions, Goddard et al. (1999) reported that juvenile cod from the northernmost part of Division 3K (Northern Peninsula, Newfoundland) develop antifreeze protein levels approximately 50% higher than cod located further south in Notre Dame, Trinity, and Conception Bays. The authors attributed these physiological differences in antifreeze production to population differences in water temperatures experienced during winter.

Movements/dispersal

Dispersal in Atlantic cod appears to be limited to the egg and larval phases of life, during which surface and near-surface water currents and turbulence are the primary determinants of horizontal and vertical displacement in the water column. For some cod populations, eggs and larvae are capable of dispersing very long distances. For example, based on the movement of satellite-tracked drifter buoys, Helbig et al. (1992) concluded that eggs spawned off southeastern Labrador (NAFO Division 2J) disperse as far south as Grand Bank. By contrast, eggs spawned by cod in inshore, coastal waters, especially at the heads of large bays, may experience dispersal distances of a few kilometres or less.

Long-term movements by cod take the form of seasonal migrations. These migrations can be attributed to geographical and seasonal differences in water temperature, food supply, and possibly spawning grounds. At one extreme, some inshore populations are suspected to have extremely short migrations, possibly limited to tens of kilometers, or less, in distance. By contrast, cod in other populations are known to traverse hundreds of kilometers during their seasonal migrations.

Good examples of long-distance seasonal migrations are those undertaken by cod in the Southern Gulf of St. Lawrence and on the Northeast Newfoundland Shelf. The former overwinter off northeast Cape Breton, migrating into the Southern Gulf in April, where they spend the summer months feeding and spawning, before returning to the deep, relatively warm waters off Cape Breton in November. Many Northeast Newfoundland Shelf cod migrate from the relatively warm offshore waters to inshore coastal waters in spring to feed primarily on capelin (*Mallotus villosus*) before returning offshore in autumn.

Movements by Atlantic cod can be inferred from mark-recapture experiments, genetic analyses, and otolith micro-chemistry. Between 1954 and 1993, a total of 205,422 cod were tagged in Newfoundland waters and released; 36,344 of these fish were recaptured by fishers (Taggart et al. 1995). Although exceedingly rare (5 of 36,344 recaptures), some cod tagged in Newfoundland waters have been recaptured in the Northeast Atlantic, although no such recaptures have been reported since the 1960s (Taggart et al. 1995). Based on this exhaustive set of tagging studies, coupled with those conducted more recently (Hunt et al. 1999; Brattey et al. 2001b), one can conclude that, with one exception, cod tend to be recaptured in the NAFO Management Area (as defined by the divisions given in Figure 4) in which they were initially tagged. The one area in which movement appears to be relatively extensive is that encompassing NAFO Divisions 3Ps, 3N, 3O, and 3L along the southeastern coast of Newfoundland and including Grand Bank. However, notwithstanding the rather extensive movements that relatively few cod undertake, genetic and otolith micro-chemical analyses are consistent with the hypothesis that these cod exist as separate populations in the Northwest Atlantic (Bentzen et al. 1996; Ruzzante et al. 1998; Campana et al. 1999; Beacham et al. 2002).

Nutrition and interspecific interactions

Atlantic cod have an extraordinarily catholic diet (Scott and Scott 1988). As larvae, they feed primarily on zooplankton (copepods and amphipods). As cod grow, they tend to feed on larger and larger prey. Immediately after the larval stage, small crustaceans, mysid shrimp, and euphausiids feature prominently in the cod diet. Once their gape is large enough, cod begin feeding on fish, including other cod (Scott and Scott 1988; Bogstad et al. 1994). Fish that have been recorded in cod stomachs have included the following: capelin, sand lance (*Ammodytes americanus*), herring (*Clupea harengus*), redfish (*Sebastes* sp.), Arctic cod (*Boreogadus saidus*), cunners (*Tautogolabrus adspersus*), alewives (*Alosa pseudoharengus*), haddock (*Melanogrammus aeglefinus*), winter flounder (*Pseudopleuronectes americanus*), mackerel (*Scomber scombrus*), shannies (*Lumpenus maculatus*, *Stichaeus punctatus* and *Ulvaria subbifurcata*), silversides (*Menidia menidia*), and sculpins (*Cottus* sp.). In addition to fish, adult cod will also consume squid, mussels, clams, whelks, tunicates, comb jellies, brittle stars, sand dollars, sea cucumbers, and polychaetes.

Although studies are few, it is clear, given the wide variety of prey consumed by cod, that to varying degrees cod compete with other species for their food.

There is no firm evidence that food availability is a limiting factor affecting the recovery of this species in Canadian waters, particularly given the historically low levels of abundance at which the species exists throughout much of its range.

However, given the considerable uncertainty that exists in contemporary estimates of the abundance of capelin off Newfoundland and Labrador (DFO 2000, 2001), it is difficult to assess the degree to which capelin may or may not be limiting the recovery of cod in the Newfoundland & Labrador population. Nonetheless, it has been hypothesized that one of the primary sources of food for adult cod in the Newfoundland & Labrador population—capelin—may be limiting in northern areas (Rose and O'Driscoll 2002), thus affecting recovery.

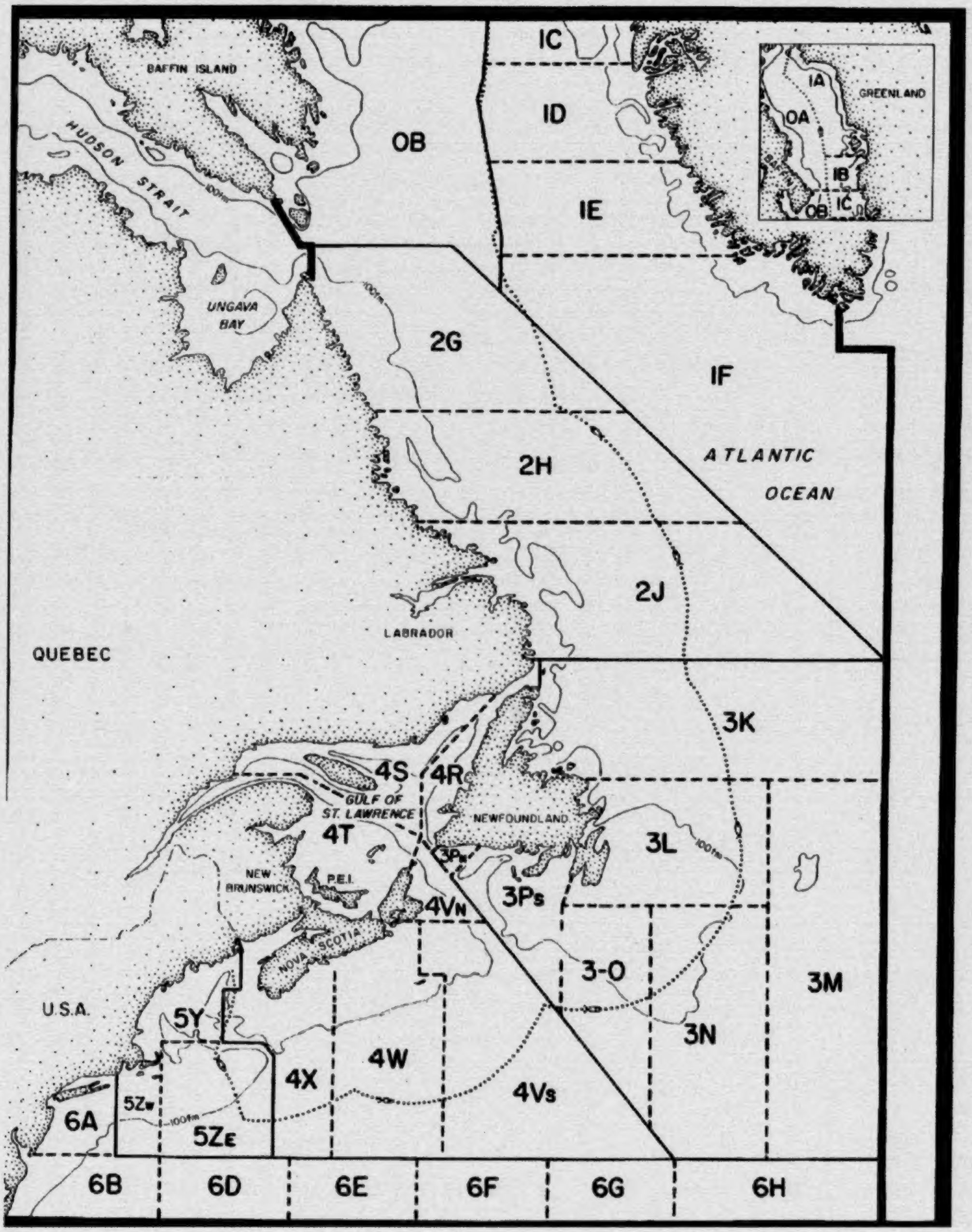

BAFFIN ISLAND
HUDSON STRAIT
UNGAVA BAY
QUEBEC
LABRADOR
NEWFOUNDLAND
GULF OF ST. LAWRENCE
NEW BRUNSWICK
P.E.I.
NOVA SCOTIA
U.S.A.
ATLANTIC OCEAN
GREENLAND
OB
IC
ID
IE
IF
IA
IB
OA
2G
2H
2J
3K
3L
3M
3N
3-O
3Ps
3Pn
4R
4S
4T
4Vn
4Vs
4W
4X
5Y
5Zw
5Ze
6A
6B
6D
6E
6F
6G
6H
100fm

Figure 4. Map showing the NAFO (Northwest Atlantic Fishery Organization) divisions used to identify stocks of Atlantic cod managed by NAFO and the Canadian Department of Fisheries and Oceans.

Behaviour/adaptability

Atlantic cod are generalists. Given that cod almost certainly exist as more than one evolutionarily significant unit in Canada, reflected to some degree by the populations proposed here, it would be reasonable to predict that cod populations respond differently to anthropogenic influences, the most obvious (and best-studied) being fishing. Such differential population responses may be reflected by differential responses to population collapse and fishery closures. For example, despite their close proximity, and reasonably higher interchange of individuals (Brattey et al. 2001a,b), the St. Pierre Bank population in the Gulf/Maritimes population recovered relatively rapidly while the adjacent Newfoundland and Labrador population has shown no signs of recovery at all (see POPULATION SIZES AND TRENDS below).

Of potential relevance to the reproductive success of Atlantic cod are the potentially negative effects that offshore gas and oil exploration may have on spawning behaviour and recruitment. Much of the present oil production and gas exploration activities occur on Grand Bank and the Scotian Shelf. Recent studies (identified above) suggest that auditory communication among cod during spawning may be of considerable importance to mate choice and reproductive success in this species. If so, then anthropogenic activities, ranging from fishing activities to exploratory drilling, that disrupt the aquatic medium in which sound so effectively travels may deleteriously affect reproductive behaviour and fertilization success in Atlantic cod. Although such effects, if present, may not be detectable during periods of high cod abundance, they may contribute to an Allee Effect when populations are low. However, until these hypotheses have been tested empirically, their merit cannot be evaluated.

POPULATION SIZES AND TRENDS

Estimates of the size of the breeding part of the population for Atlantic cod are available from two sources. The first set of estimates is derived from Virtual Population Analysis, or VPA, an analysis reliant on commercial fishery catch data and incorporating assumptions concerning the magnitude of natural, or non-fishing, mortality. Increasingly, VPAs also include estimates of the proportional representation of mature fish by age. Regarding information on breeders, one of the outputs of a VPA model is an estimate of the number of spawning individuals. The second means of estimating the size of Atlantic cod breeding populations is to use the catch rates of cod of reproductive age as determined from the annual research surveys conducted by the Department of Fisheries and Oceans (DFO).

The primary utility of VPA estimates of abundance is that they allow one to express breeding population size in the same units (numbers of individuals) for each stock or population. The main weaknesses associated with VPA estimates of abundance are that they rely upon accurate reporting of commercial catch data, they do not account for the illegal practices of discarding and catch misreporting, and they depend upon reliable estimates of mortality due to natural causes. The primary strength associated with research survey estimates of the size of the breeding population is that the data are obtained from random samples of cod caught throughout the geographical area of each stock. Thus, they are unbiased and do not depend upon the validity of assumptions concerning natural mortality and the accuracy of commercial fishery data. Unfortunately, differences among the survey areas in the catchability of cod (the proportion of cod available to be caught by the survey gear that is actually caught by that gear), coupled with differences in survey gear, prevent one from comparing the absolute values of survey catch rates among populations. In addition, survey estimates can be unduly variable in some areas in some years, leading one to conclude that survey catch rates may provide more reliable estimates of abundance trends for some stocks (e.g., Southern Gulf of St. Lawrence cod) than for others (e.g., St. Pierre Bank cod).

For the population trends described below, the ages of fish in each breeding population were $\geq$ 5 years for all stocks, except $\geq$ 4 years for Western Scotian Shelf/Bay of Fundy cod and $\geq$ 3 years for Georges Bank cod.

Generation time, as usually applied by COSEWIC (Appendix C; Organization and Procedures Manual, May 2003), is the average age of parents in the current cohort. However, COSEWIC notes that among species for which generation time varies under threat, generation time should be that estimated for the species during the pre-disturbance state. Under these circumstances, for exploited species, age at maturity can be estimated as (age at first reproduction + $1/M$), where M is the instantaneous rate of mortality due to natural events, and age at first reproduction is approximated by the age at which 50% of the adults are mature. M is thought to be 0.2 for cod in an unfished state (Smedbol et al. 2002).

I estimated the rate of decline from the slope of the linear regression of $\log_e$ abundance (N_t) versus time (t, in years), as recommended by the Marine Fishes Specialist Subcommittee at its January 2002 meeting and as adopted by DFO in its recent compilation of cod stock decline rates (Smedbol et al. 2002). The resulting regression equation is $\ln(N_t) = \alpha + \beta^*t$. The percentage decline over t years can be calculated as $(1-\exp(\beta^*t))^*100$. This method is illustrated below for the Newfoundland and Labrador population.

DFO has estimated area of occupancy for each of the stocks it manages in two ways (Smedbol et al. 2002). One, called the design-weighted area of occupancy, or DWAO, most closely approximates the definition of area of occupancy used by COSEWIC. The second is defined as the minimum area containing 95% of the cod, or D_{95}. Both indices are based on the fisheries-independent research survey data collected annually by DFO.

Because of its concordance with COSEWIC's definition of area of occupancy, only the analyses of the DWAO data will be reported here. Although this index should provide reliable estimates of the rate of decline in area of occupancy, the estimates of area of occupancy used in the analyses represent *under*-estimates of the actual areas of occupancy.

The status report recommends the identification of four populations of Atlantic cod (Figure 5).

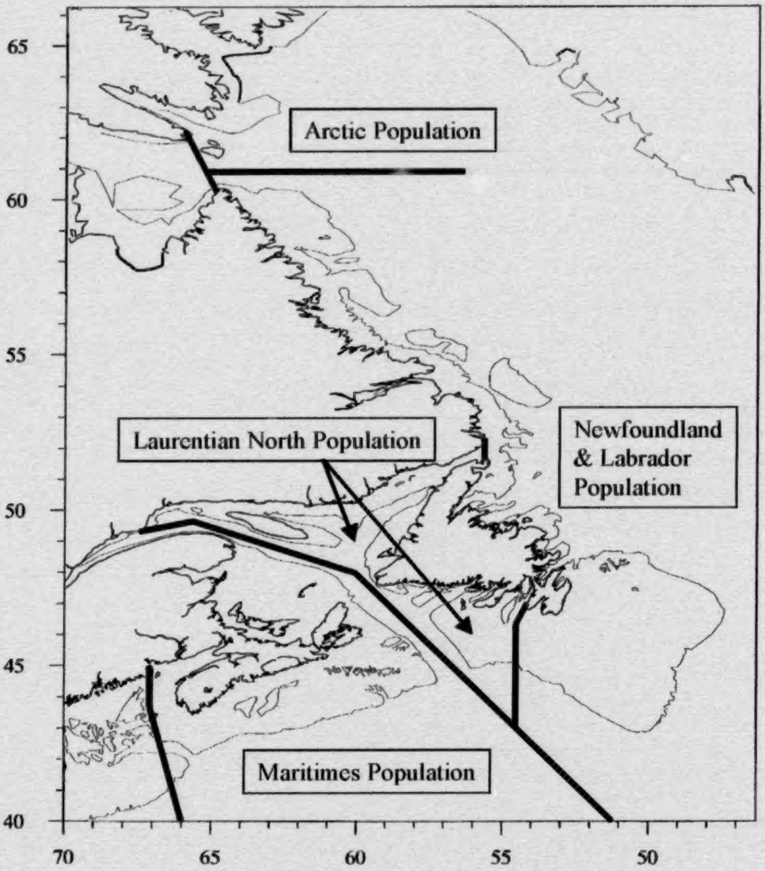

Arctic Population
Laurentian North Population
Newfoundland & Labrador Population
Maritimes Population
65
60
55
50
45
40
70
65
60
55
50

Figure 5. Distribution of Atlantic cod in Canadian waters. Boundaries of the Arctic, Newfoundland & Labrador, Laurentian North, and Maritimes populations are delineated by heavy lines. The depth contour is at 200 metres.

Arctic Population

Cod in this population are those inhabiting waters within and to the east of Baffin Island, Nunavut (marine waters are in NAFO Divisions 0A, 0B). Although little is known about cod inhabiting the marine waters in this area, they may be the ancestral source of relict landlocked populations of cod known or suspected to inhabit 7 lakes that receive intermittent tidal intrusions of salt water (Table 1). The best-studied of these lake populations is that inhabiting Ogac Lake, a salt, meromictic lake on Baffin Island that receives influxes of seawater only during the highest summer tides (McLaren 1967; Patriquin 1967). The estimated abundance of reproductive cod in Ogac Lake was approximately 500 individuals in 1962 (Patriquin 1967).

Although there are no genetic data available for cod in this population, lake-dwelling individuals are considerably larger on average than those found elsewhere in Canadian waters. In 1952, Storrs McCall and Arthur Dawson of McGill University captured a considerable number of cod from Ogac Lake, including one that measured 135 cm (25.2 kg) and one measuring 141 cm (Bruemmer 1966). In the 1960s, Patriquin (1967) reported sizes at maturity of 65 and 85 cm for Ogac Lake males and females, respectively, lengths that are 20 to 40 cm greater than sizes at maturity reported elsewhere (Brander 1994). The maximum size of cod captured in Ogac Lake in 1965 was 144 cm, and large-sized cod continued to exist in Ogac Lake in the 1980s and 1990s (see table below). Cod in excess of 1 metre in length have also been captured in the Nettilling Fjord Lake, near Pangnirtung in Cumberland Sound. One cod captured there in August 1998 is reported to have been 138 cm long, 25 kg in weight, and 13+ years in age (personal communication from Margaret Treble, DFO, Winnipeg, to David Hardie, Dalhousie University, Halifax).

Although there are no data on temporal trends in abundance, increased angling pressure has been identified as a concern by local inhabitants. Indeed, studies since the 1960s have remarked on the extraordinary ease with which large numbers of cod can be captured from these lakes. For example, in Nettilling Fjord Lake, 500 kg of cod (n=25), or 0.5 tonnes, were caught in only 1 hour of handlining (20 hooks fished for 1 hour) in August, 1985 (Lewis 1989). In 1986, 240 kg of cod (n=104) were removed from the same lake by 24 hooks fished for 1 hour (Lewis 1989).

Lake	**Date**	**Length (mean ± SD)**	**Maximum length (estimated age)**	**Source**
Ogac Lake	19 July 1999	49.9 ± 16.7 cm; n=23	111 cm (8+ yr)	DFO Winnipeg
Ogac Lake	Feb/ Mar 1987	64.3 ± 17.3 cm; n=21	107 cm (ages NA)	DFO Winnipeg
Nettilling Fjord	Sept 1985	61.0 ± 10.3 cm; n=25	102 cm (16+ yr)	Lewis (1989)
Nettilling Fjord	6-7 Aug 1986	62.0 ± 9.3 cm; n=104	77 cm (17 yr)	Lewis (1989)
Nettilling Fjord	Aug 1989	55.1 ± 8.4 cm; n=100	102 cm (ages NA)	DFO Winnipeg

Table 1. Reported locations of landlocked Atlantic cod in Nunavut.

Lake	Location	Source
Ogac Lake (also known as Ogak Lake and Ney Harbour) CONFIRMED	Across Frobisher Bay, 117 km from Iqaluit at the head of Ney Harbour (62°51'N, 67°20'W; NTS map 025J14).	McLaren (1967); Amarak Hunters and Trappers' Office (HTO), Iqaluit
Qasigialiminiq CONFIRMED	First lake on south arm of Nettilling Fjord; across from Pangnirtung and deeper into Cumberland Sound (66°02'N, 68°12'W; NTS map 026K00).	Pangnirtung HTO; Margaret Treble (DFO, Winnipeg); Dan Pike (North Atlantic Marine Mammal Commission, Tromsö, Norway, formerly of DFO, Iqaluit)
Tariuja CONFIRMED	First lake on north arm of Brown Inlet, just west from Nettilling Fjord (65°29'N, 67°20'W; NTS map 026G00).	Margaret Treble
Lake(s) on Broughton Island (now Qikiqtarjuaq) CONFIRMED	North side of Cumberland Peninsula, 177 km from Pangnirtung (67°34'N, 63°54'W; NTS map 26P).	Dan Pike
Lake at north mouth of Frobisher Bay CONFIRMED	At old DFO field camp on the Beekman Peninsula, across from Brevoort Island, north of Cyrus Field Bay.	Dan Pike. The Annual Report of the FRBC (Arctic Biological Station) from 1951-52 (Calanus) mentions Ogac Lake cod and Beekman Pensinsula cod.
Lake in the vicinity of Burwell, NU UNCONFIRMED	Burwell, in the years 1947-1950?	Personal communication to Corey Morris (DFO, St. John's) from Kathleen Martin (DFO, Winnipeg).
Resolution Island, NU UNCONFIRMED	1950?	Personal communication to Corey Morris (DFO, St. John's) from Kathleen Martin (DFO, Winnipeg).

Research surveys of the marine waters off eastern Baffin Island (NAFO Divisions 0A and 0B) are infrequent and those that have been undertaken have targeted Greenland halibut (*Reinhardtius hippoglossoides*). The most recent surveys have caught exceedingly few Atlantic cod. Among 66 tows conducted in NAFO Division 0A in 1999, only 3 cod were caught (all in a single tow) (Treble et al. 2000); among 48 tows conducted in 2001, no cod were captured (Treble 2002). Similarly, among 64 tows conducted in Division 0B in 2000, only 1 cod was caught (Treble al. 2001); none was caught among the 36 tows conducted in 0B in 2001 (Treble 2002).

The suggestion that cod in Arctic marine waters exist at very low densities is supported by other information. The Pangnirtung Fisheries Consortium reports that cod are absent in Cumberland Sound. The Iqaluit Hunters and Trappers Organization reports the same for Frobisher Bay. Low densities of cod in Arctic marine waters is also suggested by McLaren's (1967) report that no cod were taken during surveys of Frobisher Bay by M/V *Calanus* in the 1950s.

Newfoundland & Labrador population

Cod in this population combine the stocks identified for management purposes by DFO as: (1) Northern Labrador cod (NAFO Divisions 2GH; (2) "Northern" cod, i.e., those found off southeastern Labrador, the Northeast Newfoundland Shelf, and the northern half of Grand Bank (NAFO Divisions 2J3KL); and (3) Southern Grand Bank cod (NAFO Divisions 3NO). Temporal trends in abundance for each of these stocks are presented separately in APPENDIX 1.

Calculated from the means for each of its constituent stocks (APPENDIX 1), generation time is estimated to be 11.0 years for this Population, yielding a three-generation time period of 33 years. Abundance data represent the sum of the VPA estimates of mature population size for each of the stocks included in this population. The time period for which data were available for both stocks was 1962 to 2001. These are the data included here for the purpose of estimating rates of population decline.

Within the northern cod stock, there are limited temporal data that allow one to evaluate trends in abundance for cod found in inshore waters. These data include: DFO research surveys conducted annually (except 1999) since 1996 over an area of 6,400 square nautical miles; hydro-acoustic surveys of cod in Smith Sound, Trinity Bay, conducted by George Rose (Memorial University of Newfoundland) since 1995; DFO-sponsored sentinel survey catch rate data obtained by fishers; and local knowledge of fish harvesters. According to DFO's inshore survey data, catch rates of cod aged 5 years and older show an overall decline (correlation coefficient between log(catch rate) and year is negative) between 1996 and 2002 (Lilly et al. MS2003, unpublished data presented at the DFO Zonal Assessment Meeting, 20 February 2003). Hydro-acoustic estimates of cod biomass in Smith Sound (where the largest spawning component of northern cod is now located), including data obtained in January 2003, also have declined in recent years, according to George Rose (personal communication, DFO Zonal Assessment Meeting, 20 February 2003). Sentinel survey gillnet catch rates throughout the inshore waters of northeastern Newfoundland in 2001 and 2002 were either the lowest or second lowest since the beginning of the fisher-conducted surveys in 1995 (DFO 2002; Jarvis and Dalley MS2003, unpublished data presented at the DFO Zonal Assessment Meeting, 20 February 2003). Sentinel survey linetrawl catch rates for Trinity and Bonavista Bays in 2001 were the lowest in the time series (DFO 2002). Ninety-five percent of fish harvesters who responded to a questionnaire sent to Professional Fish Harvesters Committees along the northeast coast of Newfoundland reported that the Sentinel catch rates corresponded closely with trends in cod abundance observed by fish harvesters (Jarvis and Stead 2001). In 2002, a majority of fish harvesters reported that commercial catch rates and sounder recordings were the same as or lower than they were in 2001, that the amount of bait fish present in 2002 was the same as or less than that in 2001, and that cod were in average to good condition in 2001 (Jarvis and Dalley MS2003, unpublished data presented at the DFO Zonal Assessment Meeting, 20 February 2003; see also Jarvis and Stead 2001).

Irrespective of the estimated age at maturity or data source, the 3-generation decline experienced by the Newfoundland & Labrador Population was 97% (Figures 6 and 7).

Age at maturity	Generation time (yr)	Data Source	Data type	Time period	Rate of change
unfished state	11.0	VPA	number of individuals	1968-2001	−97%

Area of occupancy for this population declined from approximately 365,000 km^2 in the early 1960s to approximately 290,000 km^2 in recent years, a decline of roughly 21% (Smedbol et al. 2002).

Laurentian North population

Cod in this population combine the stocks identified for management purposes by DFO as (1) St. Pierre Bank (NAFO Division 3Ps) and (2) Northern Gulf of St. Lawrence (NAFO Divisions 3Pn4RS). Temporal trends in abundance for each of these stocks are presented separately in APPENDIX 1.

Calculated from the means for each of its constituent stocks (APPENDIX 1), generation time is estimated to be 10 years for this Population, yielding a three-generation time period of 30 years.

Abundance data represent the sum of the VPA estimates of mature population size for each of the stocks included in this population. The time period for which data were available for both stocks was 1974 to 2001. These are the data included here for the purpose of estimating rates of population decline.

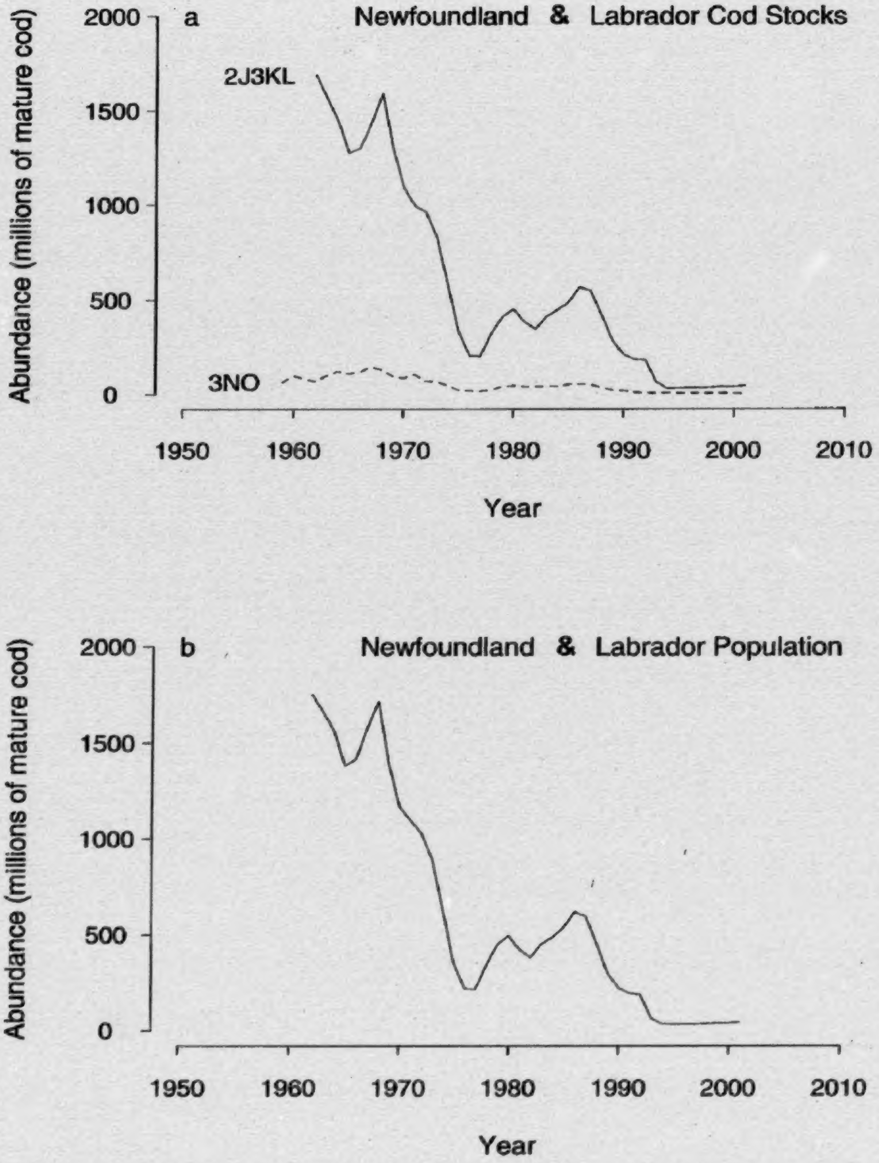


Figure 6. Temporal variation in the estimated number of mature individuals in two cod stocks in the Newfoundland & Labrador population. Data for northern cod (NAFO Divisions 2J3KL) and southern Grand Bank cod (Divisions 3NO) are shown in panel (a). The combined data for the population are shown in panel (b).

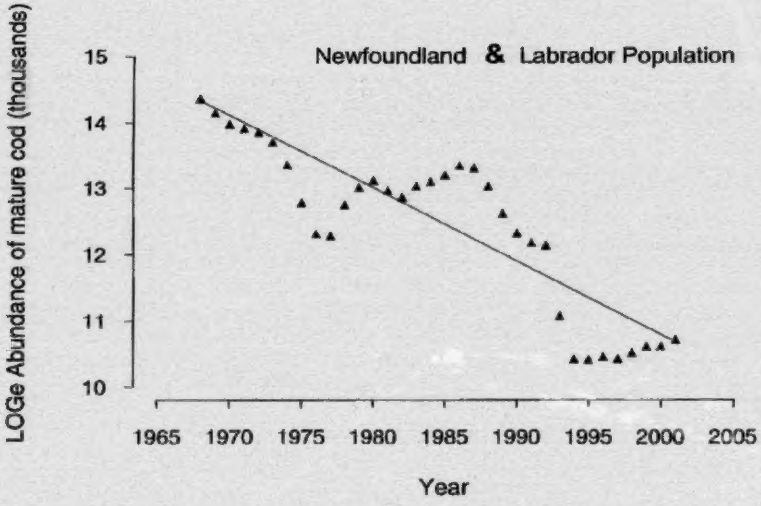


Figure 7. Plot of $\log_e$ (abundance, N_t) versus time (t, in years) for the Newfoundland & Labrador population. The line represents the linear regression equation of $\ln(N_t) = 232.19 - 0.11t$ ($r^2 = 0.77$, $p<0.0001$). Based on this equation, the rate of decline of the Newfoundland & Labrador population over the three-generation time period of 33 years is (1−exp(−0.11*33))*100, which equals 97%.

The Laurentian North population has declined 81% over the past three generations. This trend is driven primarily by the decline experienced by the Northern Gulf stock (3Pn4RS). By comparison, the St. Pierre Bank stock (3Ps) has changed relatively little since 1974 (Figure 8).

Age at maturity	Generation time (yr)	Data Source	Data type	Time period	Rate of change
unfished state	10	VPA	number of individuals	1974-2001	−81%

Area of occupancy data for this population overlap only for the years 1991 to 2001. During this period, area of occupancy declined marginally from approximately 96,000 km^2 to approximately 89,000 km^2, a decline of roughly 7% (Smedbol et al. 2002).

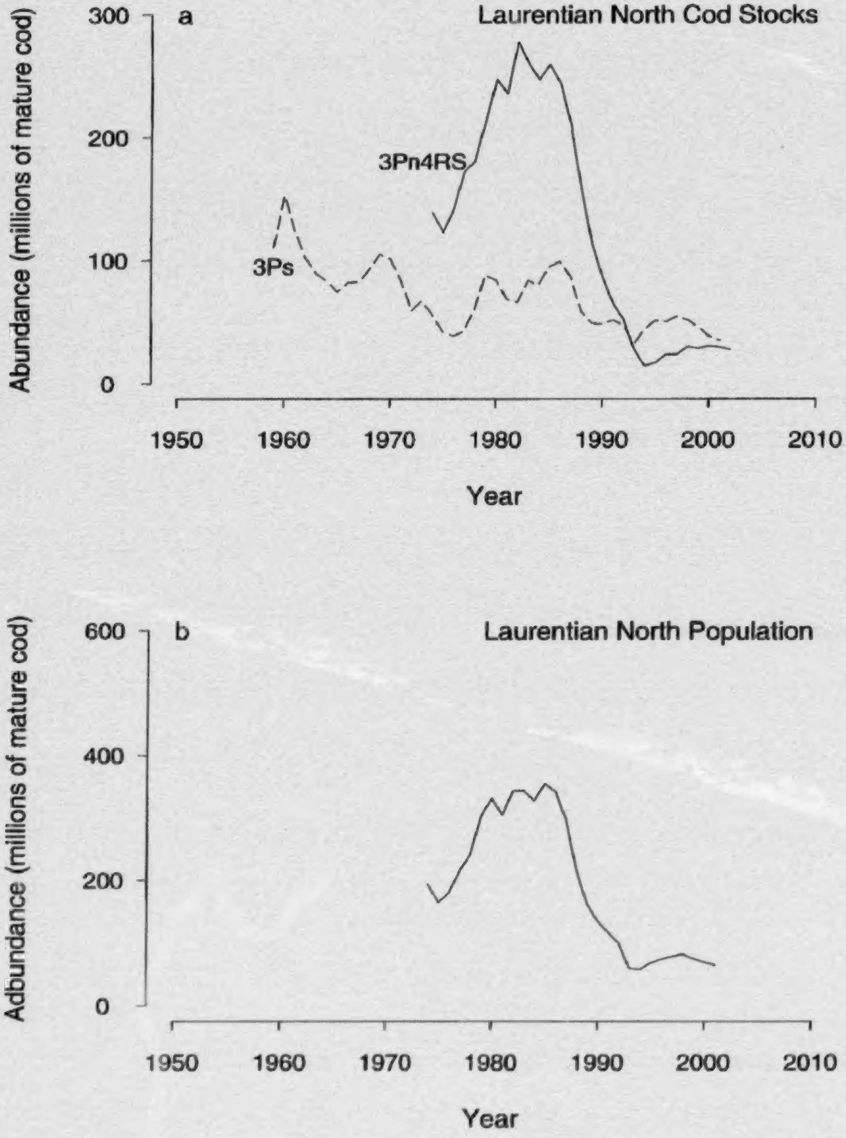


Figure 8. Temporal variation in the estimated number of mature individuals in two cod stocks in the Laurentian North population. Data for northern Gulf cod (NAFO Divisions 3Pn4RS) and St. Pierre Bank cod (Subdivision 3Ps) are shown in panel (a). The combined data for the population are shown in panel (b).

Maritimes population

Cod in this population combine the stocks identified for management purposes by DFO as: (1) Southern Gulf of St. Lawrence (NAFO Division 4T); (2) Cabot Strait (NAFO Division 4Vn); (3) Eastern Scotian Shelf (NAFO Divisions 4VsW); (4) Bay of

Fundy/Western Scotian Shelf (NAFO Division4X); and (5) cod found on the Canadian portion of Georges Bank (NAFO Division $5Ze_{j,m}$). Temporal trends in abundance for each of these stocks are presented separately in APPENDIX 1.

Calculated from the means for each of its constituent stocks (APPENDIX 1), generation time is estimated to be 9 years for this population, yielding a three-generation time period of 27 years.

Abundance data represent the sum of the VPA estimates of mature population size for each of the stocks included in this population. The time period for which data were available for most stocks was 1974 to 1997 (this being the last year in which a VPA was conducted for Eastern Scotian Shelf cod). These are the data included here for the purpose of estimating rates of population decline.

The Maritimes population has declined 14% over the past three generations. However, there is some discordance in the temporal trends among the stocks in this population (Figure 9). The dominant stock in this population (Southern Gulf; 4T) was actually at higher levels in 1997 than it was in 1974. By contrast, Eastern Scotian Shelf cod (4VsW) is (in 2002) at historically low levels, according to the research survey indices, which are not part of the present calculation.

Age at maturity	Generation time (yr)	Data Source	Data type	Time period	Rate of change
unfished state	9	VPA	number of individuals	1974-1997	−14%

Area of occupancy for this population declined from approximately 179,000 km^2 in the early 1970s to approximately 140,000 km^2, in recent years, a decline of roughly 22% (Smedbol et al. 2002).

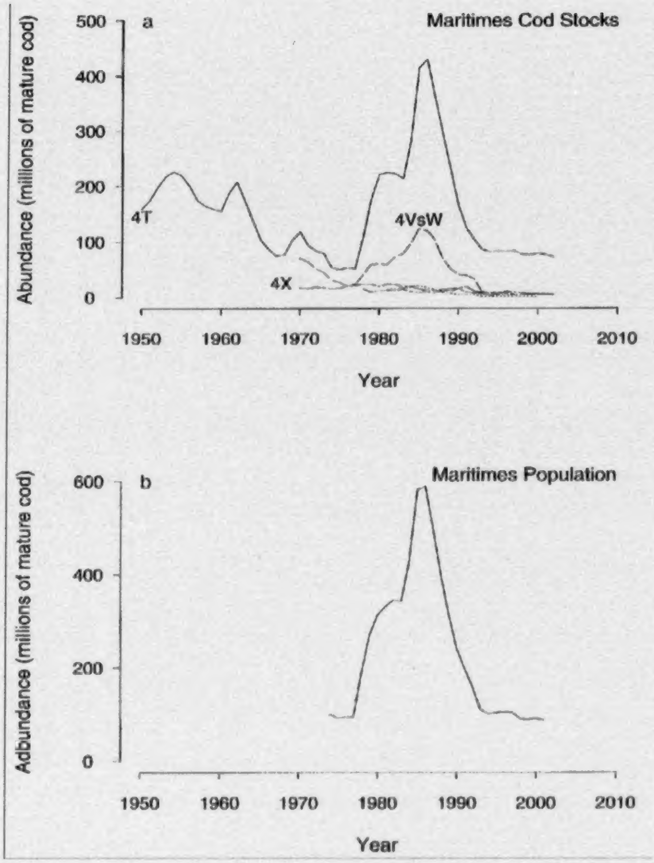


Figure 9. Temporal variation in the estimated number of mature individuals in cod stocks in the Maritimes population. Data for individual stocks, as identified in the status report, are shown in panel (a). The combined data for the population are shown in panel (b).

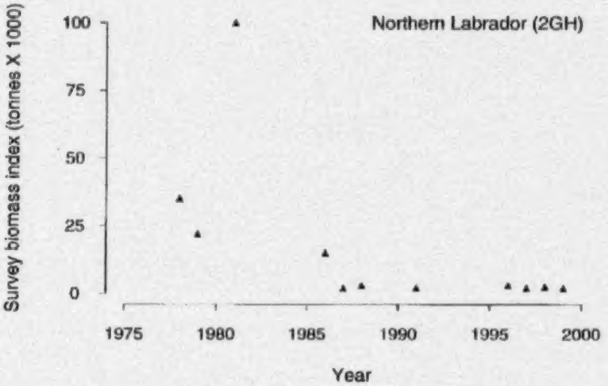


Figure 10. Temporal variation in the estimated number of mature individuals in the Northern Labrador cod stock (NAFO Divisions 2GH).

LIMITING FACTORS AND THREATS

The primary factor responsible for the decline of Atlantic cod was overfishing (Hutchings and Myers 1994; Hutchings 1996; Myers et al. 1997b; Shelton and Lilly 2000; Hutchings and Ferguson 2000a,b; Bundy 2001; Fu et al. 2001; Smedbol et al. 2002). In some areas, reductions in individual growth (Dutil and Lambert 2000; Drinkwater 2002), attributable to environmental effects or size-selective fishing mortality (Sinclair et al. 2002), may have exacerbated the rate of population decline; in some areas, increases in natural mortality may also have contributed to the decline (Dutil and Lambert 2000). It is important to note, however, that there is no evidence to suggest that the rates of growth and natural mortality experienced by cod in the 1980s were unprecedented. Although hypotheses invoking other factors have been posited, there are inadequate data that would allow for definitive tests of these hypotheses.

In theory, removal of the dominant source of anthropogenic mortality (fishing) should have resulted in population recovery. However, with one exception (St. Pierre Bank cod in the northeastern portion of the range of the Gulf/Maritimes population), recovery has not been forthcoming in the decade since the fisheries were initially closed. Empirical analyses of these issues suggest that factors other than fishing are of greater importance to recovery than fishing alone.

Recent work indicates that lack of recovery is not at all unusual among marine fish populations that experience 15-year rates of decline greater than 80% (Hutchings 2000, 2001a), even when associated with dramatic reductions in fishing mortality (Hutchings 2001b; Denney et al. submitted). However, although the factors responsible for the lack of recovery in Atlantic cod are not well understood, recent analyses implicate some combination of the following: below-average water temperatures (in some areas, in some years), fishing quotas, illegal fishing practices, bycatch, marine mammal predation, genetic changes to life history effected by fishing (see Hutchings 1999; Sinclair et al. 2002), and predation of eggs by pelagic fishes (Hutchings 1999, 2000, 2001b; Swain and Castonguay 2000; Swain and Sinclair 2000; McLaren et al. 2001; Smedbol et al. 2002).

The tremendous influence that even small catches (in the absolute sense) can have on recovery can be illustrated by considering the lack of recovery for northern cod (NAFO Divisions 2J3KL) in the Newfoundland & Labrador population. Despite having experienced declines in excess of 97%, DFO accepted the advice of the Fisheries Resource Conservation Council (www.frcc.gc.ca) and allowed directed fishing on this stock from 1999 through 2002, a measure that has had a clear and deleterious impact on the recovery of Canada's most depleted cod stock, as illustrated by the exploitation rates presented below.

Although the quotas in recent years have been small relative to those set in the mid-1980s (5,600-9,000 tonnes compared with quotas exceeding 200,000 tonnes), the impact on northern cod has been high because the size of the population is correspondingly low. This conclusion is based on mark-recapture estimates of exploitation rate analysed by DFO (DFO 2002; Brattey and Healey MS2003). A summary of these estimates is provided in the table below (these data were obtained from Table 4 in Brattey and Healey MS2003, unpublished data, presented at DFO's Zonal Assessment Meeting, Halifax, 20 February 2003).

Tagging location (northeast coast of Newfoundland)	Exploitation rates on northern cod tagged and recaptured in 1999	Exploitation rates on northern cod tagged and recaptured in 2002
Notre Dame Bay	30-63%	12-20%
Bonavista Bay	6-18%	14-19%
Trinity Bay	4-13%	10-27%

Based on these estimates of exploitation rate, one can only conclude that the northern cod quotas reintroduced in 1999 have had a negative impact on the growth and recovery of northern cod. This conclusion is based on two observations. Firstly, prior to the cod collapses in the early 1990s, it was estimated that cod populations could increase in abundance at exploitation rates less than 18%. Many of the exploitation rates reported above would, thus, permit little or no population growth. Secondly, maximum rates of population increase for northern cod have been estimated at 10 to 30% per annum (Myers et al. 1997a; Hutchings 1999). Given that the range in exploitation rate estimates typically falls within this 10-30% range of maximum population growth, population recovery will not occur, irrespective of the number of individuals in the population.

Based on the proceedings of a DFO workshop held in St. John's, Newfoundland, in March 2000 (Swain and Castonguay 2000), the lack of recovery of Atlantic cod in Canadian waters south of Cape Chidley can be attributed to:

1. Collapsed age structure, loss of spawning components (e.g., the spring-spawning component on the Eastern Scotian Shelf), and/or reduced area occupied by spawners;
2. Below-average recruitment rate in some parts of the range (Southern Grand Bank, St. Pierre Bank, Eastern and Western Scotian Shelf), but not others (NE Newfoundland Shelf, Northern and Southern Gulf of St. Lawrence);
3. Higher-than-expected natural mortality of adults in some parts of the range of each population;
4. Decline in individual growth rate in some areas within each population.

If physical structure is critically important to the survival of juvenile cod, notably in the form of plants, bottom heterogeneity, and corals, then reductions in suitable habitat may also be affecting recovery. The reduction in physical heterogeneity on the bottom, and the loss of potentially important deep-sea corals, can be attributed to the bottom-trawling gear used to catch groundfish (Collie et al. 1997, 2000; Kaiser and de Groot 2000). In Canadian waters, it has been reported that bottom-trawling may have relatively little impact on invertebrate macrofauna inhabiting sandy bottoms (Kenchington et al. 2001), although similar studies on the potential effects of trawling on fishes and fish habitat have not been undertaken (but see Mortensen et al. submitted).

Regarding predation by marine mammals, an independent expert panel concluded that the recoveries of northern cod in the Newfoundland & Labrador population and that of northern Gulf cod in the Laurentian North population have been negatively affected by seal predation (McLaren et al. 2001).

The possibility that the intense fishing pressure experienced by cod in the late 1980s and early 1990s resulted in genetic changes to heritable life history traits cannot be discounted. There is evidence to suggest that age at maturity and growth rate is lower in several cod stocks at present than it was prior to the stock collapses (Smedbol et al. 2002). The observed changes in age at maturity cannot be explained as phenotypic responses (Hutchings 1999), leaving genetic responses to selection (selecting against late-maturing genotypes) as the most parsimonious explanation for the earlier maturity observed in some areas. Similarly, smaller weights-at-age among cod in some areas can also be explained as a result of selection against fast-growing genotypes during periods of intensive fishing (see Sinclair et al. 2002). Of course, in order to test these hypotheses of genetic change, one would have to compare, in a common-garden experiment, the ages at maturity and growth rates of random samples of genotypes before and after the selection event (i.e., fishing in the late 1980s and early 1990s). The obvious unavailability of the former renders the testing of these hypotheses impossible.

In summary, the primary cause of the reduction of Atlantic cod throughout its range was over-exploitation; in some areas, the rate of decline may have been exacerbated by reductions in individual growth and apparent increases in natural mortality. Identifiable threats to the recovery of Atlantic cod include directed fishing (a consequence of the setting of quotas), indirected fishing (a consequence of illegal fishing, catch misreporting, discarding), and bycatch from other fisheries for bottom-dwelling species. Additional threats to recovery include altered biological ecosystems, and concomitant changes to the magnitude and types of species interactions (such as an increase in cod mortality attributable to seal predation). These ecosystem-level changes appear to have resulted in increased mortality among older cod. Selection against late maturity and rapid growth rate, induced by previously high rates of exploitation, may also be contributing to the higher mortality (effected by earlier maturity; Beverton et al. 1994) and slower growth observed in some areas today.

SPECIAL SIGNIFICANCE OF THE SPECIES

Given its historical and contemporary importance to society, few species have been of greater significance in Canada. After the short-lived Viking-based settlements on Newfoundland's Northern Peninsula in the late tenth century, it was cod that brought the first Europeans to Newfoundland waters in the late fifteenth century, an economic venture that spawned one of the first permanent settlements in British North America (1612; Cupids, Newfoundland). Until the early 1990s, Atlantic cod was the economic mainstay for Newfoundland and Labrador, as it was for a large part of the population in the Maritimes and along Quebec's north shore and Gaspé Peninsula. From a biological perspective, the Atlantic cod, which numbered approximately 2.5 billion spawning individuals as recently as the early 1960s (see Figure 12), was one of the dominant species of the marine food web in the Northwest Atlantic.

EXISTING PROTECTION OR OTHER STATUS

In Canada, Atlantic cod is protected federally by the *Fisheries Act* and by the *Oceans Act*. Several of the cod populations in Canadian waters are managed jointly with other countries. For example, the Georges Bank cod stock (NAFO Division $5e_{j,m}$) is jointly managed by Canada's DFO and the National Marine Fisheries Service in the United States. The cod stocks inhabiting the Newfoundland & Labrador population and the offshore waters of the Arctic population are managed jointly by Canada and international fishing nations, such as Russia, Portugal and Spain, under the auspices of the Northwest Atlantic Fisheries Organization (NAFO).

Other Status Designations: IUCN: Vulnerable; Global Heritage Status Rank: G5.

SUMMARY OF STATUS REPORT

The report suggests that Atlantic cod in Canada be recognized as four populations, in accordance with known genetic, ecological, and demographic data, and in accordance with the guidelines detailed in Appendix F5 of COSEWIC's Organization and Procedures Manual (Version 16, April 2002).

Regarding the assignment of risk, only the primary cause of the reduction in Atlantic cod (fishing) can be deemed reversible and understood. However, fishing has not ceased in any of the populations (although it is restricted in some parts of some Populations, such as Eastern Scotian Shelf). In the Laurentian North population, excessive fishing mortality has reduced the breeding part of the population, particularly in the Northern Gulf section of this population. For the Newfoundland & Labrador population, it is evident, based on harvest rates estimated by DFO, that fishing is delaying recovery in parts of this population's range.

There are several additional factors that may influence one's perception of risk.

The first concerns the downgrading of risk when there is a possibility of 'rescue', that is, immigration to the population under consideration from another population. It is not clear that such a downgrading is warranted when the neighbouring population(s) is(are) also at risk. In the present case, there are no data that would allow one to evaluate the levels of immigration or emigration into or out of the Arctic population.

While cod movement from the eastern part of the Laurentian North population (i.e., St. Pierre Bank) into the southern part of the Newfoundland & Labrador population has been documented, it is not clear that these individuals contribute significantly, either demographically or genetically, to the latter Population. Indeed, the complete absence of recovery in the southern part of the Newfoundland & Labrador population would suggest that such contributions are minimal. Regarding the Maritimes population, rescue is possible from American populations of cod in the extreme southern part of the population, although these stocks are also at low levels.

A second factor that might influence perception of risk pertains to changes in the life history of cod in some parts of its Canadian range, notably for the Newfoundland & Labrador population. The exploitation rates experienced by cod in the late 1980s and early 1990s were sufficiently high to effect genetic selection responses to life history traits, possibly favouring earlier maturity (Hutchings 1999) and slower growth (Sinclair et al. 2002) as a consequence. From an evolutionary perspective, an extended number of reproductive events per lifetime is essential for genotypic, and population, persistence in Atlantic cod. In the early 1960s, when cod aged 10 years and older were contributing more than 50% of the eggs to the Northern cod stock (Hutchings and Myers 1994), part of the Newfoundland & Labrador population, the expected number of lifetime reproductive events may well have been as much as 10 on average, and certainly more than 5. Given the absence of cod aged 10 years on the Northeast Newfoundland Shelf in recent years, the expected number of lifetime reproductive events for cod in this area is clearly less than 5 and may well be as few as 2 or 3. This considerable reduction in lifetime breeding events can be expected to have rather serious consequences for the persistence of this and other similarly affected populations, irrespective of the absolute numbers of individuals in each population.

There is another reason not to be complacent about the apparently high numbers of mature cod in Canadian waters, despite (in some cases) extraordinary declines in abundance. Although the absolute numbers of cod in each population appears high, it is important to acknowledge that census estimates of mature individuals (Nc) do not reflect the actual numbers of individuals that contribute genes during spawning, as reflected by the effective population size (Ne). For broadcast spawning organisms such as Atlantic cod, it has been estimated that Ne is 2 to 5 orders of magnitude lower than Nc because of the increased variance in individual reproductive success associated with this type of mating system (Hedgecock 1994). Empirical support for this range in Ne/Nc has recently been forthcoming from studies of marine fishes.

For example, based on estimates of Ne from declines in heterozygosity and temporal fluctuations in allele frequency over 46-48 years, Hauser et al. (2002) concluded that effective population size in the broadcast spawning New Zealand snapper (*Pagrus auratus*) was 5 orders of magnitude less than census population sizes (which number in the millions). The effective number of female red drum (*Sciaenops ocellatus*) in the Gulf of Mexico, estimated from both mitochondrial (Turner et al. 1999) and microsatellite DNA (Turner et al. 2002), is 10^{-3} that of the female census population size. In other words, based on an Ne/Nc of 10^{-3}, although one might count 1 million breeding individuals in a population, the number of individuals contributing genes to future generations would actually be 1,000.

When assessing risk for the Laurentian North population, it is important to note that the two stocks in this population have previously shown positive signs of recovery following severe reductions in fishing pressure. This is in contrast to cod in other areas, such as the Newfoundland & Labrador population and the Eastern Scotian Shelf component of the Maritimes population, where reductions in fishing pressure have not been associated with recovery. Also, current levels of abundance in the St. Pierre Bank portion of this population are not unprecedented.

For the Maritimes population, one factor that may mitigate extinction risk is the observation that the present abundance of the primary cod stock in this population (Southern Gulf of St. Lawrence) is not unprecedented. Recent declines in some parts of the population may be inflated because of unusually high abundance levels in the 1980s. Again, this is particularly true for Southern Gulf cod for which the long-term (1950-2002, about 5 generations) decline is 35% (Smedbol et al. 2002). In addition, both the mean age of spawners and the proportional representation of old fish in the Southern Gulf stock are at historically (1950-2001) high levels (Swain and Chouinard 2000; Smedbol et al. 2002).

In contrast, however, within one of the stocks in this population (Eastern Scotian Shelf) the proportional representation of large, old cod is very low (Paul Fanning, DFO, Dartmouth, personal communication). Indeed, in the absence of fishing, survey catch rates have declined precipitously between 1998 and 2002. Also of potential worry is the observation that length at 50% maturity has declined from 40 (1979-1984) to 33 cm (1997-2002) in Division 4W and from 42 (1979-1984) to 37 cm (1997-2002) in Division 4Vs (Paul Fanning, DFO, Dartmouth, unpublished data). For a species that typically does not reach maturity until it has attained a size of 50 cm (Brander 1994), these unexplained declines in size at maturity can be expected to have a negative influence on population recovery.

TECHNICAL SUMMARY

[Scientific name] *Gadus morhua*
[Common name (English)] Atlantic cod [Common name (French)] Morue franche
[Population name] Arctic Population
[Range of Occurrence in Canada (by province / territory / ocean)] Nunavut / Arctic Ocean

Extent and Area information	
• *extent of occurrence (EO)(km²)*	Marine portion: approx. 50,000 km^2; Lakes portion: < 100 km^2
• *specify trend (decline, stable, increasing, unknown)*	Unknown
• *are there extreme fluctuations in EO (> 1 order of magnitude)?*	Unlikely
• *area of occupancy (AO) (km²)*	Marine portion: unknown Lakes portion: < 100 km^2
• *specify trend (decline, stable, increasing, unknown)*	Unknown
• *are there extreme fluctuations in AO (> 1 order magnitude)?*	Unlikely
• *number of extant locations*	Marine portion: unknown Lakes portion: 5-7
• *specify trend in # locations (decline, stable, increasing, unknown)*	Stable
• *are there extreme fluctuations in # locations (>1 order of magnitude)?*	Unlikely
• *habitat trend: specify declining, stable, increasing or unknown trend in area, extent or quality of habitat*	Unknown
Population information	
• *generation time (average age of parents in the population) (indicate years, months, days, etc.)*	Marine portion: unknown Lakes portion: > 8 years
• *number of mature individuals (capable of reproduction) in the Canadian population (or, specify a range of plausible values)*	Marine portion: unknown Lakes portion: probably numbering in the hundreds in each lake
• *total population trend: specify declining, stable, increasing or unknown trend in number of mature individuals*	Unknown
• *if decline, % decline over the last/next 10 years or 3 generations, whichever is greater (or specify if for shorter time period)*	Unknown
• *are there extreme fluctuations in number of mature individuals (> 1 order of magnitude)?*	Unlikely

• *is the total population severely fragmented (most individuals found within small and relatively isolated (geographically or otherwise) populations between which there is little exchange, i.e., ≤ 1 successful migrant / year)?*	Marine portion: Unlikely Lakes portion: Yes; the probability of migration among lakes, or between the lakes and marine portions of the population, is probably nil
• *list each population and the number of mature individuals in each*	Lakes portion: Ogac (~ 500); Qasigialiminiq; Tariuja; unnamed lake on Qikiqtarjuaq; unnamed lake on Beekman Peninsula; unnamed lake near Burwell; unnamed lake on Resolution Island
• *specify trend in number of populations (decline, stable, increasing, unknown)*	Unknown
• *are there extreme fluctuations in number of populations (>1 order of magnitude)?*	Unlikely
Threats (actual or imminent threats to populations or habitats) [add rows as needed]	
- increased angling pressure in some lakes - small population sizes	
Rescue Effect (immigration from an outside source)	Marine portion: low Lakes portion: none
• *does species exist elsewhere (in Canada or outside)?*	Yes
• *status of the outside population(s)?*	Newfoundland & Labrador Population is at historically low levels; Greenland cod are also at historically low levels
• *is immigration known or possible?*	Possible for marine portion; not possible for lakes portion
• *would immigrants be adapted to survive here?*	Probably
• *is there sufficient habitat for immigrants here?*	Probably
Quantitative Analysis	None

[Scientific name] *Gadus morhua*
[Common name (English)] Atlantic cod [Common name (French)] Morue franche
[Population name] Newfoundland & Labrador Population
[Range of Occurrence in Canada (by province / territory / ocean)] Newfoundland and Labrador / Atlantic Ocean

Extent and Area information	
• *extent of occurrence (EO)(km^2)*	Approx. 620,000 km^2
• *specify trend (decline, stable, increasing, unknown)*	Declining
• *are there extreme fluctuations in EO (> 1 order of magnitude)?*	No
• *area of occupancy (AO) (km^2)*	Approx. 300,000 km^2
• *specify trend (decline, stable, increasing, unknown)*	Declining
• *are there extreme fluctuations in AO (> 1 order magnitude)?*	No
• *number of extant locations*	Unknown
• *specify trend in # locations (decline, stable, increasing, unknown)*	Unknown
• *are there extreme fluctuations in # locations (>1 order of magnitude)?*	Unknown
• *habitat trend: specify declining, stable, increasing or unknown trend in area, extent or quality of habitat*	Unknown
Population information	
• *generation time (average age of parents in the population) (indicate years, months, days, etc.)*	11 years
• *number of mature individuals (capable of reproduction) in the Canadian population (or, specify a range of plausible values)*	Approx. 45,000,000
• *total population trend: specify declining, stable, increasing or unknown trend in number of mature individuals*	Declining
• *if decline, % decline over the last/next 10 years or 3 generations, whichever is greater (or specify if for shorter time period)*	97%
• *are there extreme fluctuations in number of mature individuals (> 1 order of magnitude)?*	No
• *is the total population severely fragmented (most individuals found within small and relatively isolated (geographically or otherwise) populations between which there is little exchange, i.e., $\leq$ 1 successful migrant / year)?*	No
• *list each population and the number of mature individuals in each*	Northern cod stock: ~43,000,000 Southern Grand Bank stock: ~2,000,000

- *specify trend in number of populations (decline, stable, increasing, unknown)*	Number of stocks is stable; number of putative populations within each stock is probably declining
- *are there extreme fluctuations in number of populations (>1 order of magnitude)?*	Unlikely
Threats (actual or imminent threats to populations or habitats) [add rows as needed]	
- directed commercial and recreational fishing (suspended in 2003) - fisheries bycatch - illegal fishing and other sources of unreported catches - fishing-induced and natural changes to the ecosystem - predation on cod aged 2 yr and older by seals and fish on the northern cod stock - alteration to bottom habitat is a possible but unevaluated threat	
Rescue Effect (immigration from an outside source)	Low
- *does species exist elsewhere (in Canada or outside)?*	Yes
- *status of the outside population(s)?*	Laurentian North population is at a low level
- *is immigration known or possible?*	Yes
- *would immigrants be adapted to survive here?*	Probably
- *is there sufficient habitat for immigrants here?*	Probably
Quantitative Analysis	None

[Scientific name] *Gadus morhua*
[Common name (English)] Atlantic cod [Common name (French)] Morue franche
[Population name] Laurentian North Population
[Range of Occurrence in Canada (by province / territory / ocean)] Newfoundland and Labrador, Quebec / Atlantic Ocean

Extent and Area information	
• *extent of occurrence (EO)(km²)*	Approx. 155,000 km²
• *specify trend (decline, stable, increasing, unknown)*	Declining
• *are there extreme fluctuations in EO (> 1 order of magnitude)?*	No
• *area of occupancy (AO) (km²)*	Approx. 90,000 km²
• *specify trend (decline, stable, increasing, unknown)*	Declining
• *are there extreme fluctuations in AO (> 1 order magnitude)?*	No
• *number of extant locations*	Unknown
• *specify trend in # locations (decline, stable, increasing, unknown)*	Unknown
• *are there extreme fluctuations in # locations (>1 order of magnitude)?*	Unknown
• *habitat trend: specify declining, stable, increasing or unknown trend in area, extent or quality of habitat*	Unknown
Population information	
• *generation time (average age of parents in the population) (indicate years, months, days, etc.)*	10 years
• *number of mature individuals (capable of reproduction) in the Canadian population (or, specify a range of plausible values)*	Approx. 63,000,000
• *total population trend: specify declining, stable, increasing or unknown trend in number of mature individuals*	Declining
• *if decline, % decline over the last/next 10 years or 3 generations, whichever is greater (or specify if for shorter time period)*	81%
• *are there extreme fluctuations in number of mature individuals (> 1 order of magnitude)?*	No
• *is the total population severely fragmented (most individuals found within small and relatively isolated (geographically or otherwise) populations between which there is little exchange, i.e., ≤ 1 successful migrant / year)?*	No
• *list each population and the number of mature individuals in each*	Northern Gulf cod stock: ~28,000,000 St. Pierre Bank stock: ~35,000,000
• *specify trend in number of populations (decline, stable, increasing, unknown)*	Number of stocks is stable

• *are there extreme fluctuations in number of populations (>1 order of magnitude)?*	Unlikely
Threats (actual or imminent threats to populations or habitats) [add rows as needed]	
- directed commercial and recreational fishing (suspended on the Northern Gulf stock in 2003) - fisheries bycatch - illegal fishing and other sources of unreported catches - fishing-induced and natural changes to the ecosystem - predation by seals and fish on the Northern Gulf stock - alteration to bottom habitat is a possible but unevaluated threat	
Rescue Effect (immigration from an outside source)	Low
• *does species exist elsewhere (in Canada or outside)?*	Yes
• *status of the outside population(s)?*	Newfoundland & Labrador population is at historically low levels; abundance of the Maritimes population appears to be stable along the northern limit of this population
• *is immigration known or possible?*	Yes
• *would immigrants be adapted to survive here?*	Probably
• *is there sufficient habitat for immigrants here?*	Probably
Quantitative Analysis	None

[Scientific name] *Gadus morhua*
[Common name (English)] Atlantic cod [Common name (French)] Morue franche
[Population name] Maritimes Population
[Range of Occurrence in Canada (by province / territory / ocean)] Quebec, New Brunswick, Prince Edward Island, Nova Scotia / Atlantic Ocean

Extent and Area information	
• *extent of occurrence (EO)(km²)*	Approx. 250,000 km^2
• *specify trend (decline, stable, increasing, unknown)*	Declining
• *are there extreme fluctuations in EO (> 1 order of magnitude)?*	No
• *area of occupancy (AO) (km²)*	Approx. 160,000 km^2
• *specify trend (decline, stable, increasing, unknown)*	Declining
• *are there extreme fluctuations in AO (> 1 order magnitude)?*	No
• *number of extant locations*	Unknown
• *specify trend in # locations (decline, stable, increasing, unknown)*	Unknown
• *are there extreme fluctuations in # locations (>1 order of magnitude)?*	Unknown
• *habitat trend: specify declining, stable, increasing or unknown trend in area, extent or quality of habitat*	Unknown
Population information	
• *generation time (average age of parents in the population) (indicate years, months, days, etc.)*	9 years
• *number of mature individuals (capable of reproduction) in the Canadian population (or, specify a range of plausible values)*	Approx. 88,000,000
• *total population trend: specify declining, stable, increasing or unknown trend in number of mature individuals*	Declining
• *if decline, % decline over the last/next 10 years or 3 generations, whichever is greater (or specify if for shorter time period)*	14%
• *are there extreme fluctuations in number of mature individuals (> 1 order of magnitude)?*	No

• *is the total population severely fragmented (most individuals found within small and relatively isolated (geographically or otherwise) populations between which there is little exchange, i.e., ≤ 1 successful migrant / year)?*	No
• *list each population and the number of mature individuals in each*	Southern Gulf stock: ~72,000,000 Cabot Strait stock: ~2,000,000 Eastern Scotian Shelf stock: ~5,000,000 Western Scotian Shelf/Bay of Fundy stock: ~5,000,000 Georges Bank stock: ~4,000,000
• *specify trend in number of populations (decline, stable, increasing, unknown)*	Number of stocks is stable; number of putative populations within each stock is probably declining
• *are there extreme fluctuations in number of populations (>1 order of magnitude)?*	Unlikely
Threats (actual or imminent threats to populations or habitats) [add rows as needed]	
- directed commercial and recreational fisheries on Western Scotian Shelf/Bay of Fundy and Georges Bank stocks (suspended elsewhere) - fisheries bycatch - illegal fishing - biological changes to the species composition of the Northwest Atlantic - alteration to bottom habitat is a potential but unevaluated threat	
Rescue Effect (immigration from an outside source)	Low
• *does species exist elsewhere (in Canada or outside)?*	Yes
• *status of the outside population(s)?*	Laurentian North population is low in abundance; the Georges Bank stock in the United States is also at an historically low level of abundance
• *is immigration known or possible?*	Yes
• *would immigrants be adapted to survive here?*	Probably
• *is there sufficient habitat for immigrants here?*	Probably
Quantitative Analysis	No

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APPENDIX 1. Population trend data for each of the Atlantic cod management units recognized by the Department of Fisheries and Oceans

Northern Labrador (NAFO Divisions 2GH):

There are very few population abundance data available for cod in this area. The available data are complicated by the fact that surveys prior to 1986 were line transect surveys (i.e., involving non-random sampling) whereas those conducted thereafter were stratified-random surveys. The data reported here (Figure 10) are those reported by DFO in the publication authored by Smedbol et al. (2002). Based on an estimated age at maturity of 5.25 years for the period 1947 to 1950 (Smedbol et al. 2002), northern Labrador cod have declined 95% over the past three generations, based on the available data.

Northeast Newfoundland Shelf, or "Northern" Cod (NAFO Divisions 2J3KL):

The average age among individuals in the current cohort is 6.2 years, based on the survey catch rate data (Lilly et al. 1991; Peter Shelton, DFO, Newfoundland, personal communication). Based on data from the 1980s, age at 50% maturity is about 6years for northern cod (Lilly et al. 2001). Thus, in an unfished state, generation time is estimated to be 6+(1/0.2) = 11years, yielding a three-generation time period of 33 years.

The survey catch rate data are those reported by Lilly et al. (1991) and by Peter Shelton (personal communication). Abundance of the mature portion of the population, as estimated by VPA, are available from Baird et al. (1992) for the years 1962 to 1977 and from Bishop et al. (1993) for the years 1978 to 1992. Spawning population size for the years 1993 through 2001, for which VPA-based estimates are unavailable, was extrapolated from the survey-based spawner biomass index provided by Lilly et al. (1991; Fig. 13). To undertake this estimation, I first regressed the (log) survey catch rate data (numbers per tow for individuals age 5 years and older) against the (log) VPA abundance estimates for the same age classes for the years 1983 to 1992. The correlation coefficient (r=0.74) associated with this regression was significant (p=0.01). I then used this regression, incorporating the survey catch rate data from 1993 to 2001, to estimate numbers of individuals for the years 1993 to 2001.

Irrespective of the data source, the 3-generation rate of decline experienced by northern cod exceeded 95% (Figure 11).

Age (yr) at maturity	Generation time (yr)	Data Source	Data type	Time period	Rate of change
6	11	survey	catch rate (# per tow)	1983-2001	−99.9%
		VPA	numbers of spawners	1968-2001	−97%

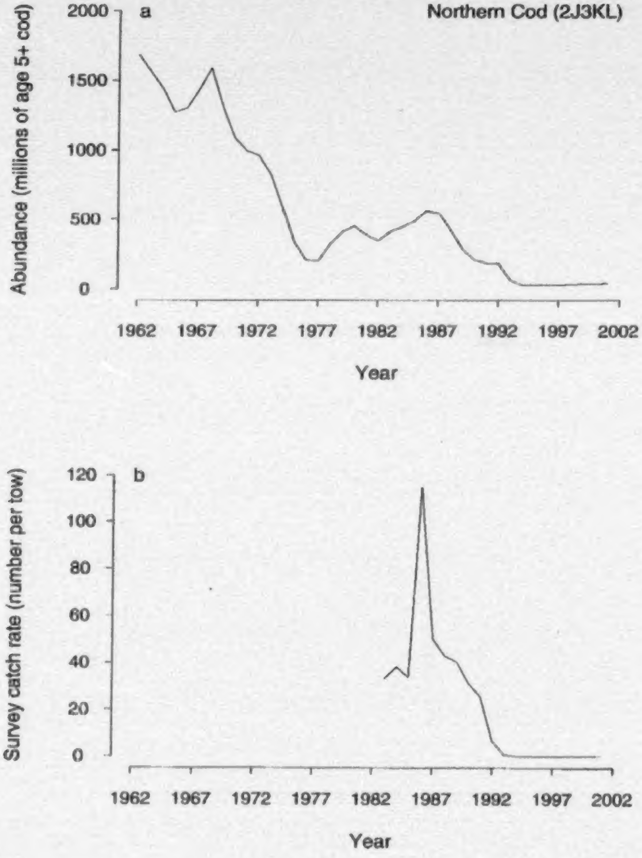

Figure 11. Temporal variation in the estimated number of mature individuals in the Northern cod stock (NAFO Divisions 2J3KL).

Among other things, this has resulted in an extraordinary decline in the overall abundance of cod in Canadian waters. In the early 1960s, approximately 75-80% of the cod in Canadian waters was located in NAFO areas 2J, 3K, and 3L (see Figure 12); in 2001, approximately 20% of Canada's cod were located in the same area. Of note is the fact that I have used ages 5 years and older for my calculation of the size of the breeding population of northern cod. The reason for doing so is based on the observation that significant numbers of cod 5 and 6 years of age in this stock are mature (Lilley et al. 2001). In contrast, recent estimates of the size of the breeding population of northern cod by DFO (Smedbol et al. 2002) included only those fish aged 7 and older. Thus, although the trends in abundance are the same, my estimates will over-estimate breeding population size while those presented by DFO can be considered under-estimates.

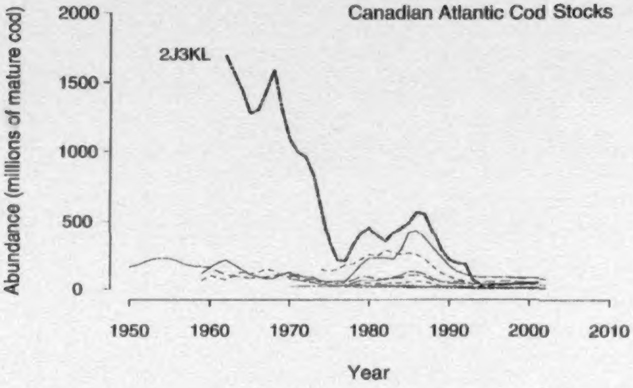

Figure 12. Temporal variation in the estimated number of mature individuals in Canada's Atlantic cod stocks, showing the size of the Northern cod stock (2J3KL), part of the Newfoundland & Labrador population, relative to the sizes of the other stocks.

Area of occupancy:

Between 1983 and 2001 (the range of the reported data), area of occupancy declined from approximately 275,000 km^2 to approximately 215,000 km^2, a rate of decline of roughly 22% (Smedbol et al. 2002).

Threats to recovery posed by fishing and marine mammal predation:

DFO has estimated that, since 1999, fishing has been removing 4 to 63% of the available northern cod, depending on the fishing region (DFO 2002; Brattey and Healey MS2003) (prior to the cod collapses in the early 1990s, it was estimated that cod populations could increase in abundance at exploitation rates less than 18%). For the northern cod stock as a whole, recent estimates of exploitation rate are in excess of 30% (Smedbol et al. 2002). Regarding predation of cod by seals, an independent Expert Panel concluded that "it is difficult to disagree with the most recent stock status assessment that 'there is a possibility that predation by seals is preventing the recovery of the cod stock'. This view is further supported by new (although highly uncertain) estimates that the consumption of cod >3 y old by hooded seals in the offshore substantially exceeds the estimated biomass" (McLaren et al. 2001).

Southern Grand Bank (NAFO Divisions 3NO):

The average age among individuals in the current cohort is 11.3 years, based on the spring survey catch rate data for 2001 (Don Stansbury, DFO, Newfoundland Region, personal communication). Based on data from the 1970s and 1980s, age at 50% maturity is about 6yr for southern Grand Bank cod (Trippel et al. 1997; Stansbury et al. 2001). Thus, in an unfished state, generation time is estimated to be 11years, yielding a three-generation time period of 33 years. The survey data are those reported by

Stansbury et al. (2001) and by Stansbury (personal communication). Abundance data for the mature part of the population, as estimated by VPA, are available from Stansbury et al. (2001). The earliest year for which survey data are available is 1984. VPA estimates of abundance extend back to 1959.

Irrespective of the data source, the 3-generation rate of decline experienced by southern Grand Bank cod exceeded 95% (Figure 13).

Age (yr) at maturity	Generation time (yr)	Data Source	Data type	Time period	Rate of change
6	11	survey	catch rate (# per tow)	1984-2001	−95%
		VPA	numbers of spawners	1968-2001	−98%

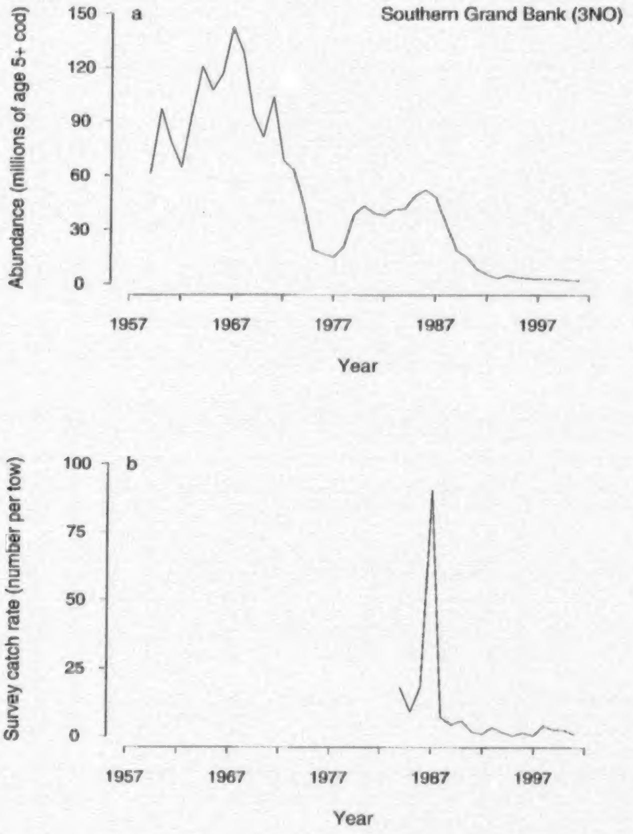

Figure 13. Temporal variation in the estimated number of mature individuals in the Southern Grand Bank cod stock (NAFO Divisions 3NO).

Area of occupancy:

Between 1984 and 2000 (the range of the reported data), area of occupancy declined from approximately 90,000 km^2 to approximately 75,000 km^2, a rate of decline of roughly 17% (Smedbol et al. 2002).

Threats to recovery posed by fishing and marine mammal predation:

In the past 5 years, exploitation rates have been low, generally estimated to be less than 5% (Smedbol et al. 2002) (prior to the cod collapses in the early 1990s, it was estimated that cod populations could increase in abundance at exploitation rates less than 18%). There is insufficient data to evaluate the threat to recovery posed by marine mammal predation on southern Grand Bank cod (McLaren et al. 2001).

St. Pierre Bank (NAFO Division 3Ps):

The average age among individuals in the current cohort is 7.3 years, based on the survey catch rate data (Brattey et al. 2001a). Based on data from the 1960s and 1970s, age at 50% maturity is about 6years for St. Pierre Bank cod (Brattey et al. 2001a). Thus, in an unfished state, generation time is estimated to be 11years, yielding a three-generation time period of 33 years. The survey data are those reported by Brattey et al. (2001). Abundance data for the mature part of the population, as estimated by VPA, are also available from Brattey et al. (2001a). The earliest year for which survey data are available is 1983. VPA estimates of abundance extend back to 1959.

The 3-generation rate of decline experienced by St. Pierre Bank cod was 47-48% (Figure 14).

Age (yr) at maturity	Generation time (yr)	Data Source	Data type	Time period	Rate of change
6	11	survey	catch rate (# per tow)	1983-2001	−47%
		VPA	numbers of spawners	1968-2001	−46%

Area of occupancy:

Between 1983 and 2001 (the range of the reported data), area of occupancy appears to have increased slightly from approximately 38,000 km^2 to approximately 45,000 km^2, a rate of increase of roughly 16% (Smedbol et al. 2002).

Threats to recovery posed by fishing and marine mammal predation:

In 2000 and 2001, exploitation rates were estimated to be approximately 20% (Smedbol et al. 2002) (prior to the cod collapses in the early 1990s, it was estimated that cod populations could increase in abundance at exploitation rates less than 18%). Marine

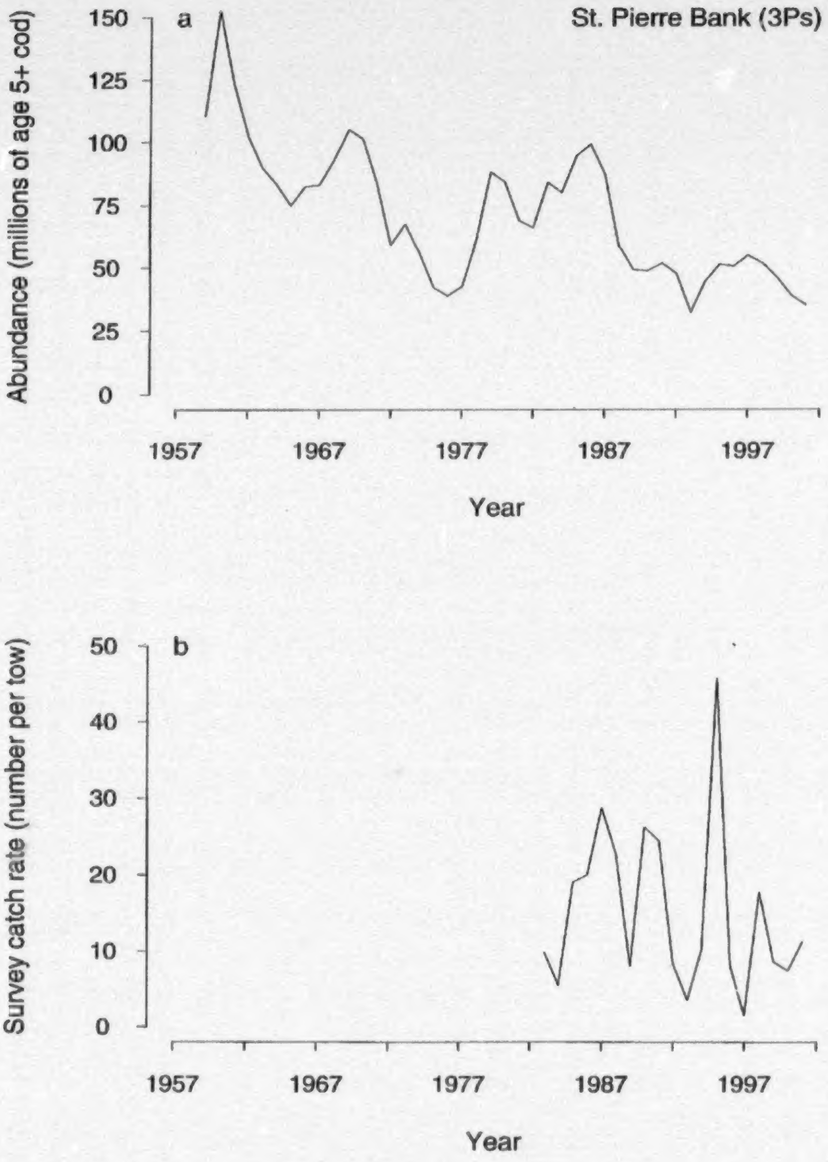

Figure 14. Temporal variation in the estimated number of mature individuals in the St. Pierre Bank cod stock (NAFO Divisions 3Ps).

mammal predation does not appear to pose a threat to recovery of St. Pierre Bank cod (McLaren et al. 2001).

Northern Gulf of St. Lawrence (NAFO Divisions 3Pn4RS):

The average age among individuals in the current cohort is 5.6 years, based on the survey catch rate data (Alain Fréchet, DFO, Mont-Joli, personal communication). Based on maturity-at-age data for the 1970s and 1980s, as estimated by Yvon Lambert (DFO, Mont-Joli), age at 50% maturity is about 4 years for northern Gulf cod. Thus, in an unfished state, generation time is estimated to be 9 years, yielding a three-generation time period of 27 years. The survey data are those estimated from the *Alfred Needler* surveys and communicated to me by Alain Fréchet, who also provided me with VPA-based abundance data for the mature part of the population. The earliest year for which survey data are available is 1990. VPA estimates of abundance extend back to 1974.

Rates of decline of Northern Gulf cod depended on the source of abundance data. Importantly, the VPA estimates were the only data that encompassed the 3-generation time frame for each of the age at maturity estimates. Rate of decline based on the VPA data is 93% (Figure 15).

Age (yr) at maturity	Generation time (yr)	Data Source	Data type	Time period	Rate of change
4	9	Survey	number of individuals	1990-2002	−64%
		VPA	numbers of spawners	1975-2002	−93%

Area of occupancy:

Between 1991 and 2001 (the range of the reported data), area of occupancy declined from approximately 58,000 km^2 to approximately 44,000 km^2, a rate of decline of roughly 24% (Smedbol et al. 2002).

Threats to recovery posed by fishing and marine mammal predation:

In the past 5 years, exploitation rates have been steadily increasing to an estimated 30% in 2001 (Smedbol et al. 2002) (prior to the cod collapses in the early 1990s, it was estimated that cod populations could increase in abundance at exploitation rates less than 18%). In addition to fishing, marine mammal predation appears to pose a threat to recovery for northern Gulf cod, as revealed by McLaren et al.'s (2001) statement: "The conclusion that seals are important predators on cod in this area appears to be inescapable".

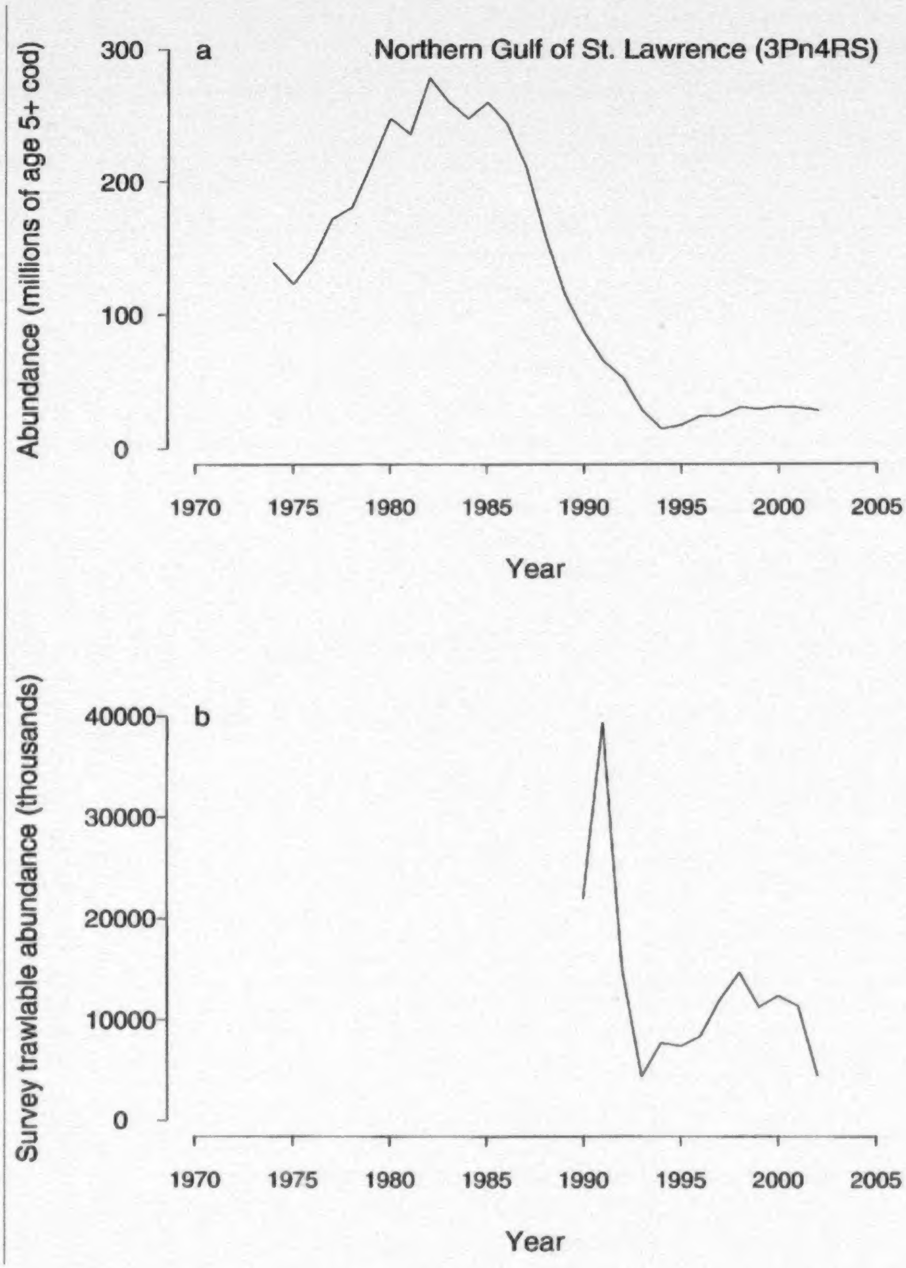

Figure 15. Temporal variation in the estimated number of mature individuals in the Northern Gulf of St. Lawrence cod stock (NAFO Divisions 3Pn4RS).

Southern Gulf of St. Lawrence (NAFO Division 4T):

The average age among individuals in the current cohort is 6.5 years, based on the survey catch rate data for 2001 (Smedbol et al. 2002). Based on data from the 1990s, age at 50% maturity is about 4.5 years for southern Gulf cod (Trippel et al. 1997; Doug Swain, DFO, Moncton, personal communication). Thus, in an unfished state, generation time is estimated to be 9.5 years, yielding a three-generation time period of 28.5 years. The survey data are those reported by Chouinard et al. (2001) and communicated to me by Doug Swain. Abundance data for the mature part of the population, as estimated by VPA, are available from Chouinard et al. (2001). The earliest year for which survey data are available is 1971. VPA estimates of abundance extend back to 1950.

Estimated rates of change for Southern Gulf cod differed with the type of abundance data, ranging from a 23% decline to a 27% increase over the past three generations. Based on the full time series of data (Figure 16), which extend back to 1950, it is clear that the current population size of Southern Gulf cod is similar to that experienced from the mid-1960s through the mid-1970s, and perhaps lower than that experienced in the 1950s.

Age (yr) at maturity	Generation time (yr)	Data Source	Data type	Time period	Rate of change
4.5	9.5	Survey	catch rate (# per tow)	1972-2001	+27%
		VPA	numbers of spawners	1973-2002	−23%

Area of occupancy:

Between 1971 and 2001 (the range of the reported data), area of occupancy increased from approximately 58,000 km^2 in the early 1970s to 65,000 km^2 in the 1980s before returning to approximately 58,000 km^2 in 2001 (Smedbol et al. 2002).

Threats to recovery posed by fishing and marine mammal predation:

Since 1999, exploitation rates have been approximately 10% (Smedbol et al. 2002) (prior to the cod collapses in the early 1990s, it was estimated that cod populations could increase in abundance at exploitation rates less than 18%). Estimates of cod consumption by seals do not seem to implicate seals in the present high adult mortality rate and lack of recovery of cod in the southern Gulf (McLaren et al. 2001).

Cabot Strait (NAFO Division 4Vn):

The average age among individuals in the current cohort is 5.2 years, based on the survey catch rate data (Mohn et al. 2001; Diane Beanlands, DFO, Dartmouth, personal communication). Based on data from the 1970s and 1980s for 4T cod, age at 50% maturity is about 4.5 years for southern Cabot Strait cod (Trippel et al. 1997).

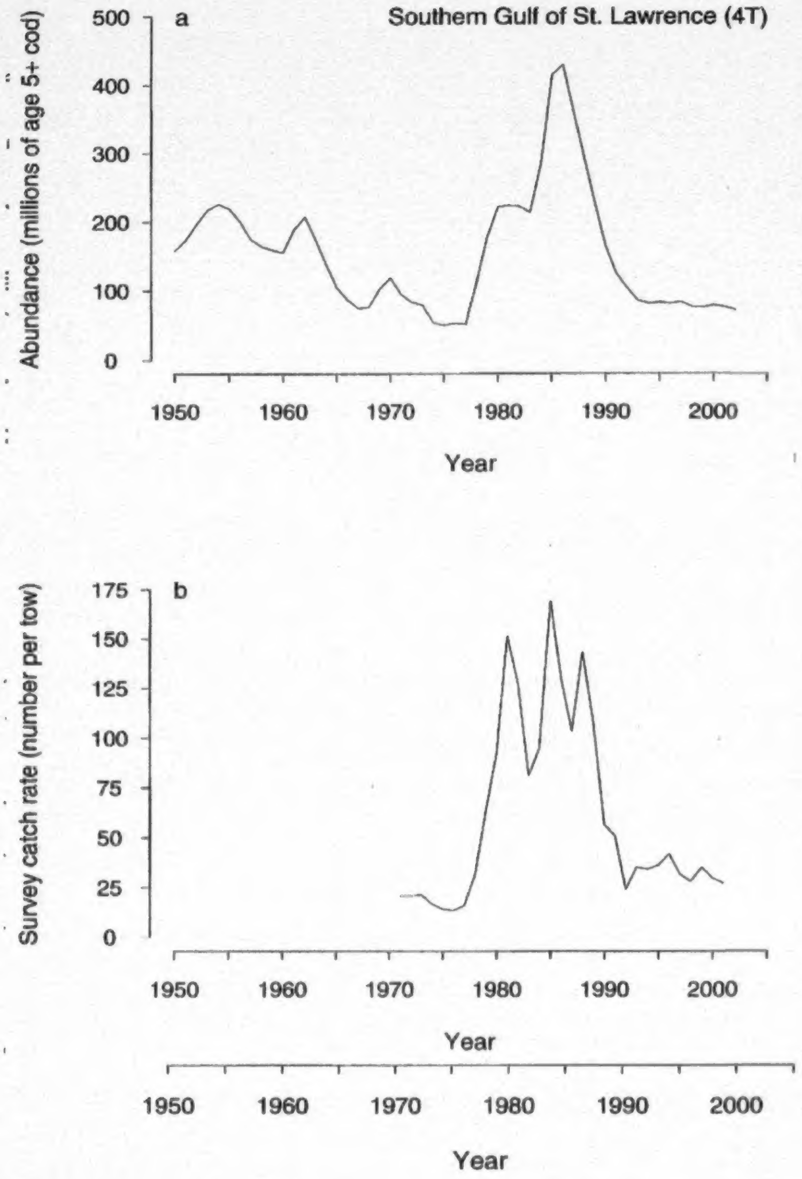

Figure 16. Temporal variation in the estimated number of mature individuals in the Southern Gulf of St. Lawrence cod stock (NAFO Division 4T).

Thus, in an unfished state, generation time is estimated to be 9.5 years, yielding a three-generation time period of 28.5 years. The survey data and VPA-based estimates of abundance are those reported by Mohn et al. (2001) and communicated to me by Diane Beanlands. The earliest year for which survey data are available is 1970. VPA estimates of abundance extend back to 1981.

The rate of decline experienced by Cabot Strait cod differs with the time period and with the type of abundance data used in the analysis. In the past 20 years, it has declined 95%, based on VPA data. The research survey data, which extend back to 1970 (Figure 17), suggest that the size of the Cabot Strait cod stock has remained stable over a 3-generation time frame.

Age (yr) at maturity	Generation time (yr)	Data Source	Data type	Time period	Rate of change
4.5	9.5	Survey	catch rate (# per tow)	1972-2001	+4%
		VPA	numbers of spawners	1981-2000	−95%

Area of occupancy:

Between 1970 and 2001 (the range of the reported data), area of occupancy remained constant at approximately 12,000 km^2 (Smedbol et al. 2002).

Threats to recovery posed by fishing and marine mammal predation:

Since 1994, exploitation rates have remained very low at approximately 2% (Smedbol et al. 2002) (prior to the cod collapses in the early 1990s, it was estimated that cod populations could increase in abundance at exploitation rates less than 18%). McLaren et al. (2001) report that there is little information with which to judge the effects of seals on Cabot Strait cod.

Eastern Scotian Shelf (NAFO Divisions 4VsW):

The average age among individuals in the current cohort is 5.8 years, based on the survey catch rate data (Mohn et al. 1998; Diane Beanlands, DFO, Dartmouth, personal communication; Paul Fanning, DFO, Dartmouth, personal communication). Based on data from the 1980s and 1990s, age at 50% maturity is about 4 years for eastern Scotian Shelf cod (Trippel et al. 1997). Thus, in an unfished state, generation time is estimated to be 9 years, yielding a three-generation time period of 27 years. The survey data are those reported by Mohn et al. (1998). Abundance data for the mature part of the population, as estimated by VPA, are available from Mohn et al. (1998). The earliest year for which survey data are available is 1970. VPA estimates of abundance extend back to 1970 and end in 1997.

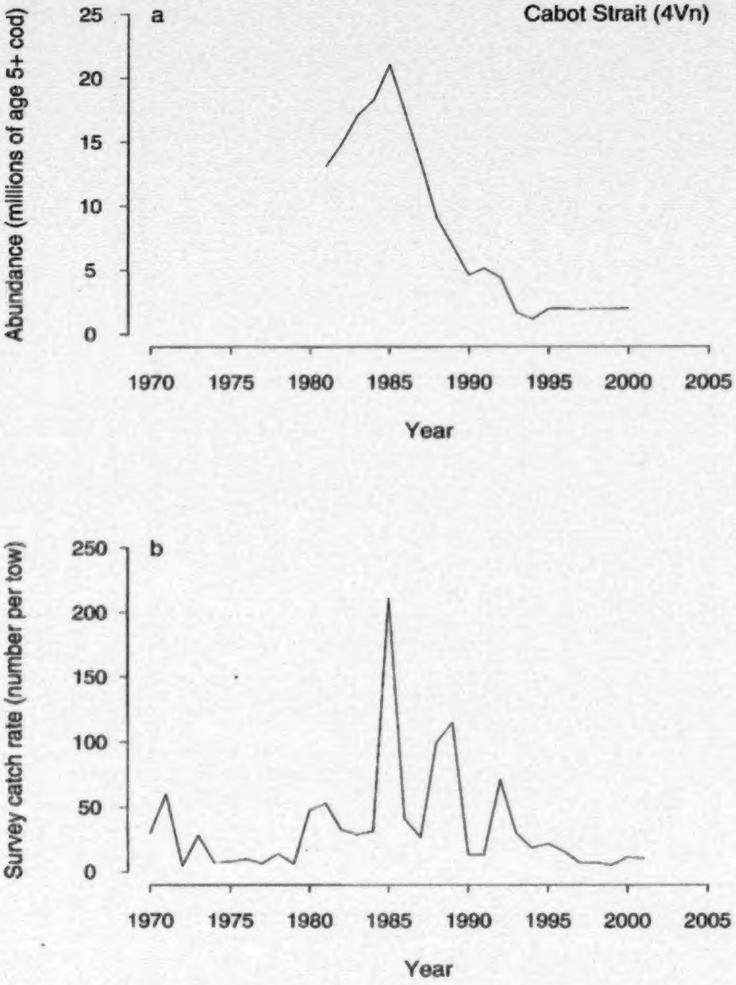

Figure 17. Temporal variation in the estimated number of mature individuals in the Cabot Strait cod stock (NAFO Division 4Vn).

The 3-generation rate of decline experienced by Eastern Scotian Shelf cod ranges between 75 and 92% (Figure 18). Indeed, in the five years since a VPA was last undertaken for this stock, survey data indicate a decline in catch rate of one order of magnitude (1998-2002 data).

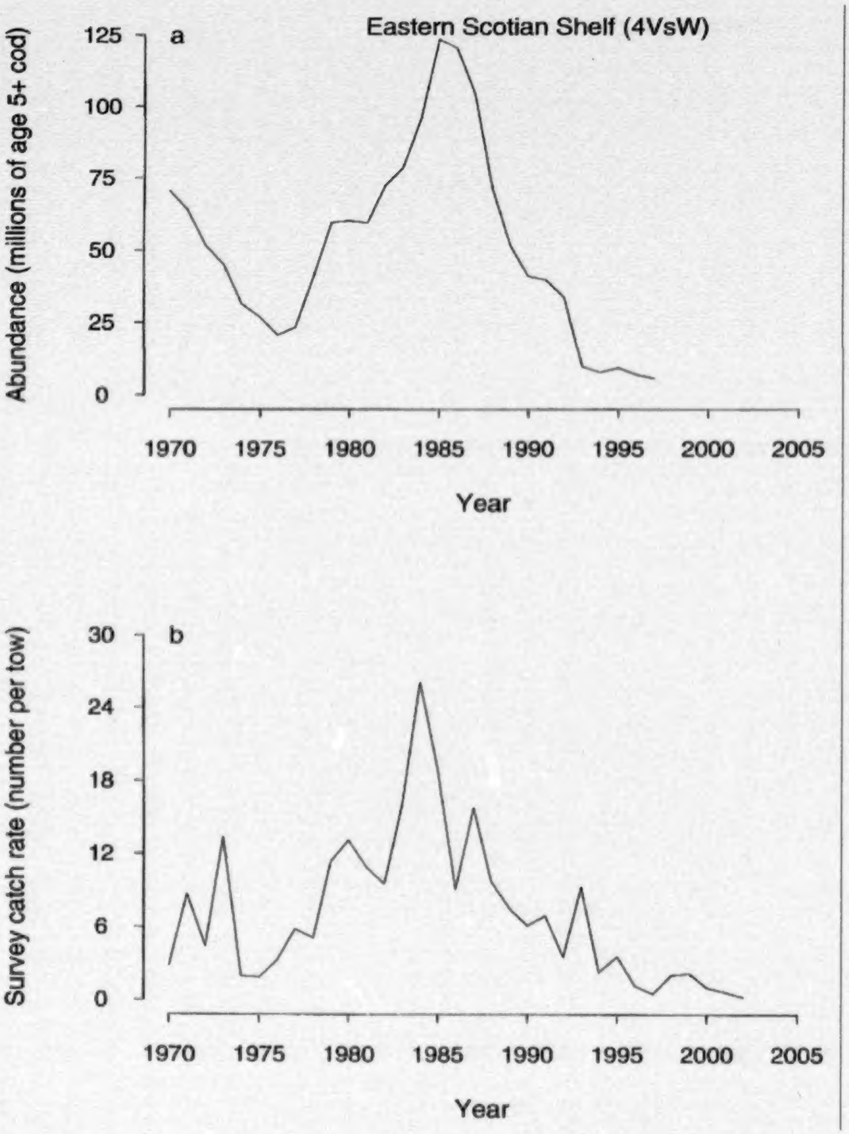

Figure 18. Temporal variation in the estimated number of mature individuals in the Eastern Scotian Shelf cod stock (NAFO Divisions 4VsW).

Age (yr) at maturity	Generation time (yr)	Data Source	Data type	Time period	Rate of change
4	9	Survey	catch rate (# per tow)	1975-2002	−92%
		VPA	numbers of spawners	1970-1997	−75%

Area of occupancy:

Between 1970 and 2000 (the range of the reported data), area of occupancy declined from approximately 65,000 km^2 to approximately 35,000 km^2, a rate of decline of roughly 46% (Smedbol et al. 2002).

Threats to recovery posed by fishing and marine mammal predation:

Since 1994, exploitation rates have remained very low at less than 2% (Smedbol et al. 2002) (prior to the cod collapses in the early 1990s, it was estimated that cod populations could increase in abundance at exploitation rates less than 18%). McLaren et al. (2001) concluded that "the overall evidence that grey seals may be preventing recovery of stocks on the Scotian Shelf is weak".

Western Scotian Shelf/Bay of Fundy (NAFO Division 4X):

The average age among individuals in the current cohort is 3.7 years, based on the survey catch rate data (Donald Clark, DFO, St. Andrews, personal communication). Based on data from the 1970s and 1980s for 4X cod, age at 50% maturity is about 2.5 years (Trippel et al. 1997). Thus, in an unfished state, generation time is estimated to be 7.5 years, yielding a three-generation time period of 22.5 years. The survey data and VPA-based estimates of abundance are those reported by and communicated to me by Donald Clark. The earliest year for which survey data are available is 1970. VPA estimates of abundance also extend back to 1970.

The 3-generation rate of decline experienced by cod on the Western Scotian Shelf and Bay of Fundy ranged between 53 and 78% (Figure 19).

Age (yr) at maturity	Generation time (yr)	Data Source	Data type	Time period	Rate of change
2.5	7.5	Survey	catch rate (# per tow)	1978-2001	−53%
		VPA	numbers of spawners	1979-2002	−78%

Area of occupancy:

Between 1970 and 2000 (the range of the reported data), area of occupancy declined slightly from approximately 45,000 km^2 to approximately 40,000 km^2, a rate of decline of roughly 11% (Smedbol et al. 2002).

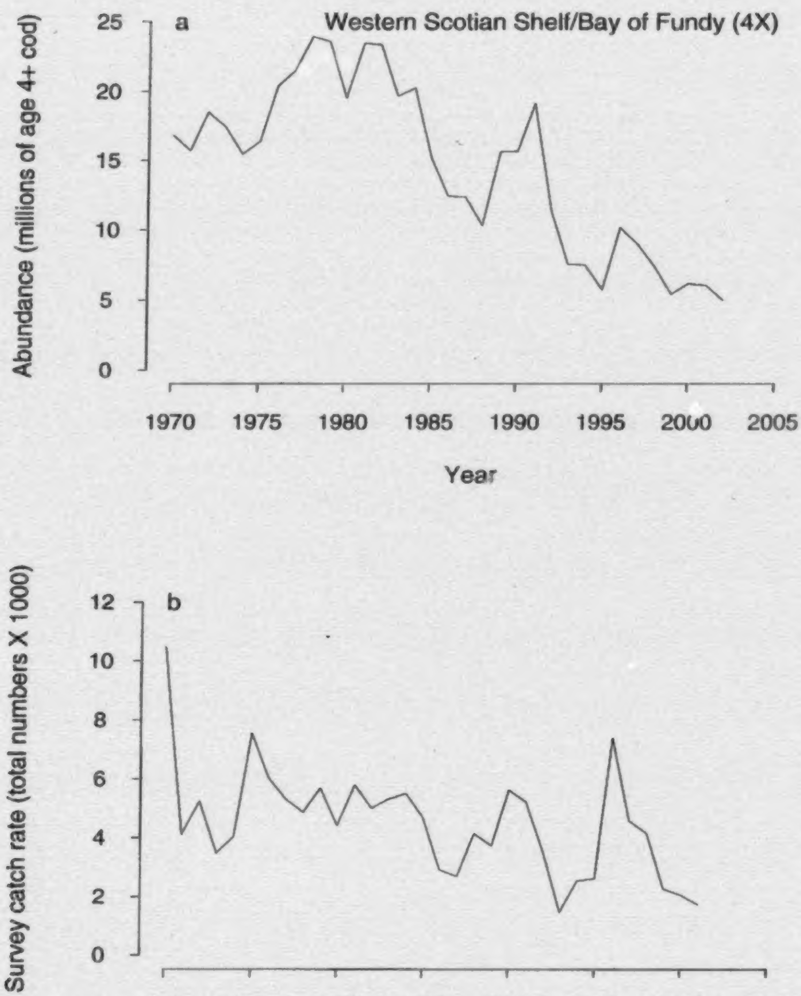

Figure 19. Temporal variation in the estimated number of mature individuals in the Western Scotian Shelf/Bay of Fundy cod stock (NAFO Division 4X).

Threats to recovery posed by fishing and marine mammal predation:

Since 1994, exploitation rates have remained close to 30% (Smedbol et al. 2002) (prior to the cod collapses in the early 1990s, it was estimated that cod populations could increase in abundance at exploitation rates less than 18%). There is little information with which to judge the threat posed by seal predation to Western Scotian Shelf/Bay of Fundy cod (McLaren et al. 2001).

Georges Bank (NAFO Division 5Zj,m):

The average age among individuals in the current cohort is 4.9 years, based on the survey catch rate data (Hunt and Hatt 2002). Based on data from the 1970s and 1980s, age at 50% maturity is about 2.5 years for Georges Bank cod (Hunt and Hatt 2002). Thus, in an unfished state, generation time is estimated to be 7.5 years, yielding a three-generation time period of 22.5 years. The survey and VPA abundance data are those reported by Hunt and Hatt (2002). The earliest year for which survey data are available is 1978 for the U.S. NMFS (National Marine Fisheries Service) fall survey and 1986 for DFO's spring survey. VPA estimates of abundance extend back to 1978.

The estimated rate of decline for Georges Bank cod differed considerably among the sources of abundance data. Estimated rates of change over three generations ranged from a 68 to 70% decline for the longest of the time series to a 5% increase for the DFO spring survey data. Although the VPA abundance data reveal a steady decline since the late 1970s, survey catch rate data available since the mid-1980s are highly variable (Figure 20).

Age (yr) at maturity	Generation time (yr)	Data Source	Data type	Time period	Rate of change
2.5	7.5	NMFS fall survey	catch rate (# per tow)	1978-2001	−68%
		DFO spring survey	catch rate (# per tow)	1986-2002	+5%
		VPA	numbers of spawners	1979-2002	−70%

Area of occupancy:

Between 1987 and 2001 (the range of the reported data), area of occupancy remained unchanged at approximately 14,000 km^2 (Smedbol et al. 2002).

Threats to recovery posed by fishing and marine mammal predation:

Since 1999, exploitation rates have declined to approximately 10% (Smedbol et al. 2002) (prior to the cod collapses in the early 1990s, it was estimated that cod populations could increase in abundance at exploitation rates less than 18%). There is little information with which to judge the threat posed by seal predation to Georges Bank cod (McLaren et al. 2001).

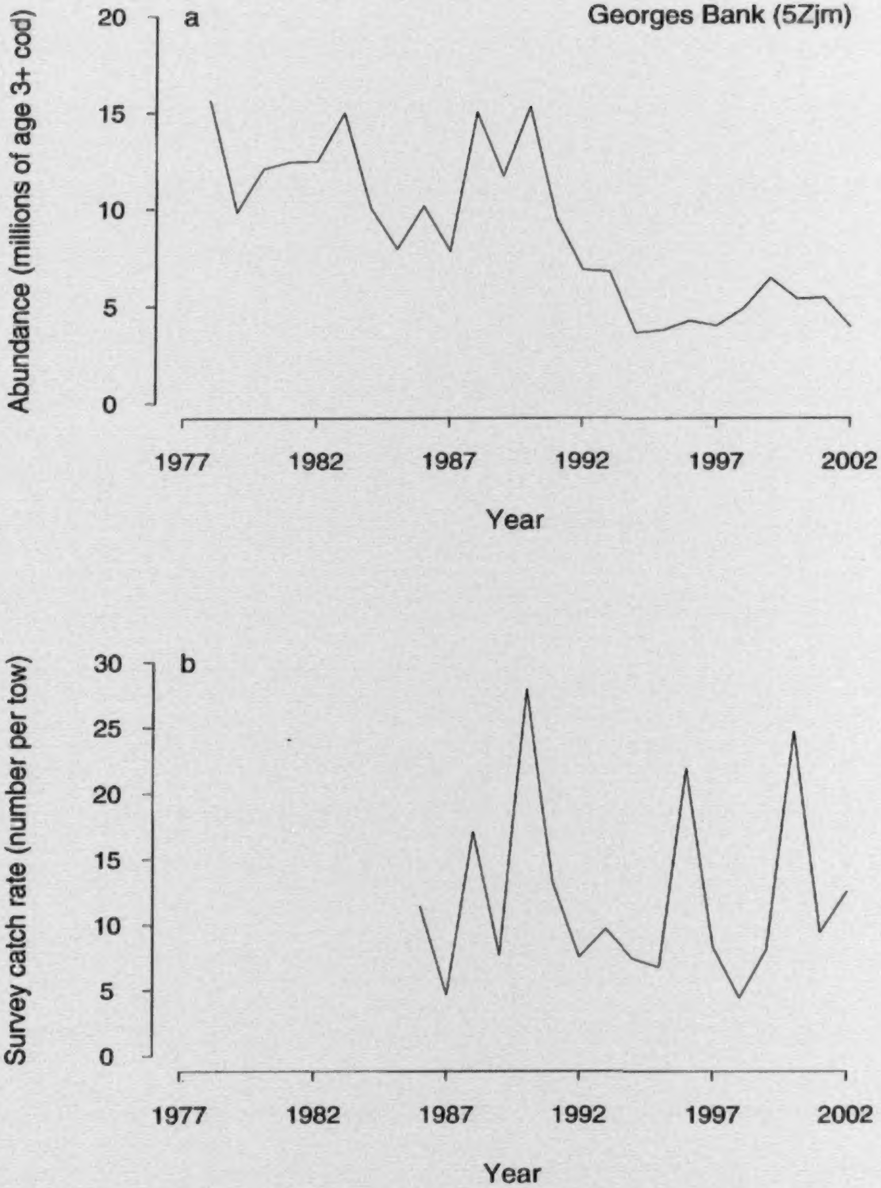

Figure 20. Temporal variation in the estimated number of mature individuals in the Georges Bank (Canadian portion) cod stock (NAFO Division 5Zj,m).